Local and global controllers of grassland ecosystem stability during global change

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Master of Science

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Pietermaritzburg
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Preface

The research contained in this dissertation was completed by the candidate while based in the School of Life Sciences in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg campus, South Africa. The research was financially supported by the Mandela Rhodes Foundation.

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.

Supervisor approval

Prof Kevin Kirkman

Dr Michelle Tedder

Declaration: Plagiarism

I, Stuart Demmer, declare that:

(i) the research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;
(ii) this dissertation has not been submitted in full or in part for any degree or examination to any other university;
(iii) this dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;
(iv) this dissertation does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
  (a) their words have been re-written but the general information attributed to them has been referenced;
  (b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced;
(v) where I have used material for which publications followed, I have indicated in detail my role in the work;
(vi) this dissertation is primarily a collection of material, prepared by myself, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included;
(vii) this dissertation does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the dissertation and in the References sections.

Signed: Stuart Demmer
Date: November 2019

Declaration: Publications

My role in each paper and presentation is indicated in **bold**.

Chapter 1

(i) **Demmer S**., Kirkman K., Tedder M., (2018a) The Diversity-Stability Debate: Do We Know the Underlying Mechanisms?, *53rd Annual Congress of the Grassland Society of Southern Africa*. Pretoria, South Africa, 67

This poster presentation informed the development of the systematic map protocol on which Chapter 1 was based. Stuart Demmer designed and presented the poster with inputs from Kevin Kirkman and Michelle Tedder.

(ii) **Demmer S**., Kirkman K., Tedder M., (2018b) What Evidence Is Available on the Drivers of Grassland Ecosystem Stability across a Range of Outcome Measurements: A Systematic Map Protocol, Environmental Evidence 7,1, 25. doi: 10.1186/s13750-018-0137-z

This publication formed the methodological foundation of Chapter 1. Stuart Demmer, Kevin Kirkman, and Michelle Tedder conceived the study. All authors defined the study boundaries based on the resources available. Stuart Demmer wrote the manuscript, designed the search strings, their quality assessment process, inclusion criteria, critical appraisal, and database coding strategy with inputs from all other authors. All authors read and approved the final manuscript.

Chapter 2

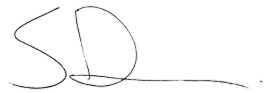
(i) **Demmer S**., Kirkman K., Tedder M., (2019a) Species losses following persistent fertilisation increase grassland stability in response to temperature variation, The Conservation Symposium 2019. Howick, South Africa

The results of this chapter were presented by Stuart Demmer. Stuart Demmer developed the presentation with inputs from Kevin Kirkman.

Chapter 3

(i) **Demmer S**., Kirkman K., Tedder M., (2019b) Environmental controllers of grassland stability responses to nutrient addition, The Conservation Symposium 2019. Howick, South Africa

The results of this chapter were presented by Stuart Demmer. Stuart Demmer developed the presentation with inputs from Kevin Kirkman.



Signed: Stuart Demmer
Date: November 2019

Dedication

For Carmen.

I waited patiently for the Lord;
he inclined to me and heard my cry.
He drew me up from the pit of destruction,
out of the miry bog,
and set my feet upon a rock,
making my steps secure.
He put a new song in my mouth,
a song of praise to our God.
Many will see and fear,
and put their trust in the Lord.

– A Psalm of David, Psalm 40:1-3

Acknowledgements

This work would not have been possible without the assistance and resources provided by so many people. Firstly, I would like to thank those who had the foresight to initiate the profound long-term ecological research experiments which were used in this dissertation. Together with this my thanks go to those who have meticulously maintained the two trials used in the experimental research chapters by applying the treatments, collecting the data and contributing to earlier reports and publications which have been vital in understanding the history of these trials.

Secondly, I wish to thank my supervisors, Kevin Kirkman and Michelle Tedder for their support during the conception and development of this dissertation. I am also grateful for their impacts on my personal development.

Thirdly, I am grateful for my friends at the University of KwaZulu-Natal who have allowed me to be involved in their work. I also wish to thank the The Mandela Rhodes Foundation which provided a wonderful opportunity to learn and grow under the guidance of challenging and dynamic leaders whilst being surrounded by inspiring peers. The Foundation has provided me with much more than tuition and living allowances – the experiences, lessons, and relationships gained from my time as a Mandela Rhodes Scholar will continue to enrich me.

Fourthly, I could not have produced any of this work without the support of the open source community. Each aspect of this dissertation was generated using numerous R and LaTeX (via TinyTeX, Thesisdown and Pandoc) packages. Almost all the skills needed to use these packages were obtained from platforms such as `stackoverflow.com`, `stats.stackexchange.com`, and `tex.stackexchange.com`. Platforms such as these are making opensource research increasingly accessible and I look forward to their future developments.

Finally, I wish to thank those closest to me. My family, who have supported me no matter my mood or commitments to my work. My parents and friends, who have been founts of incredible wisdom. Carmen, who has allowed me to grow and encouraged me to continually focus not only this project but also on other more important aspects of our blooming life together.

Soli Deo gloria.

For I consider that the sufferings of this present time are not worth comparing with the glory that is to be revealed to us. For the creation waits with eager longing for the revealing of the sons of God. For the creation was subjected to futility, not willingly, but because of him who subjected it, in hope that the creation itself will be set free from its bondage to corruption and obtain the freedom of the glory of the children of God. For we know that the whole creation has been groaning together in the pains of childbirth until now. And not only the creation, but we ourselves, who have the firstfruits of the Spirit, groan inwardly as we wait eagerly for adoption as sons, the redemption of our bodies. For in this hope we were saved. Now hope that is seen is not hope. For who hopes for what he sees? But if we hope for what we do not see, we wait for it with patience.

– Paul the apostle, Romans 8:18-25

Abstract

Human impacts on grasslands dramatically affect grassland biodiversity which impacts the ability of ecosystems to sustainably provide ecosystem services. As the extents of these anthropogenic impacts increase (due to agricultural intensification, for instance) solutions to this problem are becoming increasingly important. The ecosystem stability concept provides a framework to investigate how biological systems such as grasslands respond to disturbances. However, there is uncertainty relating to the ecosystem components which influence the various facets of ecosystem stability. Therefore, the aim of this dissertation is to 1) outline the current academic consensus pertaining to the drivers of grassland ecosystem stability, 2) contribute to underrepresented research areas identified in the literature review, and 3) investigate whether there are general environmental conditions which predispose to grassland destabilisations following anthropogenic disturbance. Academic consensus was assessed using a systematic map of review articles discussing grassland ecosystem stability concepts. This review highlighted the many complex interactions that exist in grassland ecosystems. There was also a strong consensus that diversity mediates ecosystem functioning and stability. Other ecosystem processes such as fire, herbivory, woody encroachment, and plant invasions were also well represented and discussed in these review publications, however, climatic impacts on grasslands were identified as an important knowledge gap. To address this, nutrient enriched grassland stability responses to temperature variability were studied using a long-term nutrient addition experiment. Surprisingly, nutrient enriched grassland productivity was more stable than control grasslands in response to temperature variability. Finally, environmental drivers of grassland stability changes following nutrient addition were assessed using a globally replicated experiment. This investigation showed that grasslands with a history of intensive anthropogenic management are positively affected by nutrient addition whilst stability in more naturally assembled grasslands is greatly reduced following nutrient addition. Stability changes were also associated with changes in nutrient availability and soil macronutrient (specifically Ca and K, but not micronutrient) status. Sward structure changes (such as increased compositional dissimilarity, greater dominance, and reduced asynchrony) were associated with stability reductions following nutrient addition. The findings of these three investigations highlight the serious impacts that human activities which result in increased nutrient deposition in grasslands are having on grassland ecosystems. In relation to the prevailing consensus identified in the review literature concerning the positive effects of grassland diversity on ecosystem stability and functioning, this dissertation advocates for the increased preservation of intact grasslands.

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Chapter 1

The current consensus on the drivers of grassland ecosystem stability

Abstract

Recently there has been considerable focus on the ecosystem services concept which has resulted in important advancements in biodiversity conservation at land management scales. However, many have cautioned against the ecosystem services approach because of its focus on subjectively selected aspects of the ecosystem which may not reflect long-term ecosystem dynamics. This has encouraged calls for deeper study into ecosystem functioning using an ecosystem multifunctionality framework. Here greater biodiversity is thought to facilitate greater functioning leading to more sustainable ecosystems. Although ecosystem multifunctionality is a relatively recent development, the general premise is based on the hypothesis that diversity begets stability. However, several key review syntheses have consistently called for ecosystem stability driver-outcome relationship studies to extend beyond traditional measurements. Understanding these relationships requires holistic approaches which are often challenging to investigate experimentally due to resource constraints. Systematically mapping out the relationships between various stability drivers and outcomes could provide a more empirical basis on which both the ecosystem multifunctionality and services land management frameworks could be based. This work identifies and discusses the trends in review publications which address diversity–stability related studies within the grassland biome. This review thus gives an indication of the level of consensus within the scientific community for the various drivers and outcomes of grassland ecosystem stability.

Relevant studies were sourced from the ISI Web of Knowledge database. Inclusion criteria were applied to the returned articles to identify studies relevant to the primary question; what evidence is available on the drivers of grassland ecosystem stability across a range of outcome measurements? These inclusion criteria were based on (1) subject population - the grassland biome; (2) possible ecosystem stability drivers and comparators (e.g. measures of diversity, functioning, food web connectedness, and disturbances); and (3) stability outcomes considering all measures of ecosystem stability (e.g. coefficients of variation, changes in ecosystem functionality, resistance to disturbances and invasions, return rates following disturbance). Many drivers and measurements of stability were identified across the grassland ecosystem at both aboveground and belowground levels. Key findings suggest strong support for diversity's stabilising effect on grassland productivity and promotion of ecosystem productivity. We also found strong consensus pertaining to the negative impact that some anthropogenic processes (e.g. nutrient addition and heavy grazing) have on grassland stability processes. We also point

out important areas where there is little consensus on the direction of some drivers on some outcomes (herbivory effects on plant diversity and diversity and fire effects on plant invasions).

1.1 Background

1.1.1 Ecosystem services

Ecosystems biology has seen the explosion of the ecosystem services concept over recent decades where ecosystems are studied principally to understand their socio-economic contribution to human societies (Chaudhary et al. 2015; Malinga et al. 2015). This discipline has largely formed out of the growing awareness of the anthropically-driven demand for natural resources which is driving the biodiversity crisis affecting both humans and the environment (Tilman et al. 2002; Foley et al. 2005; Godfray et al. 2010; Ceballos et al. 2015; Visconti et al. 2016). The ecosystem services concept has rapidly spread from academic arenas and is now influencing governmental policies resulting in numerous important conservation projects aimed at ensuring that the supply of these services is maintained or restored (Daily and Matson 2008; Bullock et al. 2011; Lu et al. 2012).

Ecosystem services are, however, somewhat subjectively defined and quantified, as they are based on the needs or desires of a particular human population at a given space and time and are therefore anthropogenically biased (Manning et al. 2018). Whilst this is useful for policy development (De Groot et al. 2010; Braat and de Groot 2012; Maes et al. 2012; Malinga et al. 2015), it is not useful when objectively defining or describing ecosystems and their functioning in their natural state. The danger here is that humans may be shifting their management focuses of largely undisturbed ecosystems towards those which promote only a few key beneficial or profitable services whilst other services are ignored (Manning et al. 2018). There are important ethical debates surrounding anthropocentric perspectives towards environmental management (Jax et al. 2013; Schröter et al. 2014); however, an anthropocentric approach is often key to mitigating poverty and suffering in under-resourced communities. In these scenarios Fisher et al. (2013) argued that there must be a strong focus on maintaining ecosystem services use to ensure both human and ecological community sustainability. Successful examples of this approach include alien plant clearing programmes in South Africa (Turpie et al. 2008; Shackleton et al. 2011), protected areas in Madagascar which aim to alleviate poverty, improve natural resource sustainability as well as conservation (Gardner et al. 2013), forest restoration in Vietnam (Jourdain et al. 2014), and conventional (three species intercropped) versus traditional (monocrops) farming methodology in Costa Rica (Berbes-Blazquez et al. 2017).

There have indeed been impressive positive advancements and applications of the ecosystem services concept. However, whilst highlighting the breadth of knowledge across several key scientific disciplines Abson et al. (2014) also identified a low occurrence of key sustainability terminology ($< 40\%$ of 265 key terms identified during their systematic mapping) in nine key research clusters. Mace et al. (2012) identified difficulties and confusion between biodiversity (and its associated metrices) and ecosystem services. Mace et al. (2012) reported that the terms “biodiversity” and “ecosystem services” are occasionally used interchangeably (rather than more correctly identifying biodiversity as a regulator of ecosystem services in most cases and then biodiversity being a service itself in some cases). This has likely negatively impacted how humans manage land especially considering that many interactions between biodiversity and ecosystem processes are poorly understood. This raises some issues concerning the benefit of adopting the ecosystem service approach when sustainably managing land. Although

acknowledging the importance of the ecosystem services concept in solving many problems, Norgaard (2010) similarly argued that the ecosystem services concept's rapid proliferation may blind us to the underlying complexities associated with the ecosystem services concept. This is relevant particularly from a pure ecology perspective that lacks universal or generic models that can be easily imported into economic models (Carpenter et al. 2006). Therefore, calls for further investigations to understand the complex feedback and trade-off mechanisms involved when sustainably managing land for multiple ecosystem services to meet basic human needs seem valid (Raudsepp-Hearne et al. 2010; Suich et al. 2015). In a sense, these authors recognised the limitations of applying reductionist approaches to ecosystems studies.

1.1.2 Ecosystem multifunctionality - the bridge between applied and theoretical ecology

Manning et al. (2018) recognised this problem of somewhat ambiguous ideas and definitions. Their proposed solution is an important distinction between ecosystem services and ecosystem functioning. They suggested that ecosystem services be quantified in situations where human gain and wellbeing is a primary concern, but ecosystem multifunctionality (the positive relationship between species diversity and number of functions, Hector and Bagchi 2007) be studied in more general scenarios where an objective measure of the ecosystem's overall performance is useful. Knowledge on ecosystem functioning is thus logically an important prerequisite for productive and sustainable ecosystem management.

Superficially, ecosystem functions (generally measures of vegetation production and removal, nutrient cycling, and soil microbe and plant pathogen activities, Hector and Bagchi 2007; Maestre et al. 2012; Manning et al. 2018; Soliveres et al. 2016a) do not appear to be important ecosystem services. However, investigations of the effects of land use changes on ecosystem multifunctionality revealed a marked reduction in species diversity whilst grass biomass production increased dramatically as agricultural land uses shifted from a natural state towards functionality focussed on biomass production (Allan et al. 1997; Gossner et al. 2016). Thus, communities become more similar across trophic levels as one function becomes dominant – an example of biotic homogenisation (Gossner et al. 2016).

Whilst the ecosystem multifunctionality topic is a relatively recent development (Gamfeldt and Roger 2017), it considers only the relationship between diversity and function. An agricultural setting may strive for biotic homogenisation to boost productivity in intensive agriculture. However, the danger of biotic homogenisation is more easily understood when considering the diversity-stability hypothesis which underpins the multifunctionality thesis. For several decades ecologists have hypothesised more diverse systems to be more temporally stable than less diverse systems (reviewed by Hooper et al. 2005). Larger species pools lead to more complex species interactions which may help mitigate ecological shifts during environmental perturbations (McNaughton 1977). Tilman and Downing (1994) showed in their drought resistance assessment that higher grass species diversity results in proportionately less change in biomass production during droughts. The similarities between ecosystem stability and engineering principles were then realised by Naeem and Li (1997). This idea suggests that each species (or each part in a machine) carries out a particular function that contributes to the overall functioning of the system. The more unique species present in the community, the greater the number of functions within the community. Greater species numbers can also result in an insurance effect where multiple species performing one function will allow the function to persist in the ecosystem even if some species become lost from the ecosystem (McCann 2000). Isbell et al. (2011) conducted a global analysis of how the number of species

promoting ecosystem functioning changes across space and time. They concluded that most plant species (approximately 84%) occurring in grasslands provide ecosystem services. Thus, losing only a few species could severely affect the ecosystem's sustainability and stability thereby reducing the area's ability to consistently and effectively supply ecosystem services.

1.1.3 Diversity and stability - its current relevance

The studies highlighted in the previous section suggest a strong link between species diversity and ecosystem stability which has direct or indirect effects on sustainable land management to promote ecosystem services. However, Donohue et al. (2016) showed how ecologists, environmental policymakers and practitioners differed widely in their usage of stability-related terms. This has made ecosystem stability a confusing term to grasp (Grimm and Wissel 1997) and makes measuring policy implementation success difficult to quantify and monitor. Donohue et al. (2016) proposed several solutions that could address this, an important one being developing methods to quantify the stability of whole ecological networks through time and space. Several metrices have been developed to address this (e.g. Landscape Function Analysis - Tongway and Hindley 2004, Rapid Ecosystem Function Assessment - Meyer et al. 2015). These methods are based largely on biodiversity-ecosystem functioning which, like the ecosystem multifunctionality thesis, provides a more holistic understanding of the ecosystem (Mace et al. 2012). Whilst this is an important step forward, these metrices do not actively identify the underlying mechanisms driving and sustaining biodiversity and ecosystem functioning. Combination studies addressing ecosystem stability and functioning do exist. However, these tend to study the effect of diversity on biomass production stability (for examples see Tilman et al. 2006; Reich et al. 2012; Hautier et al. 2015). Even fewer studies have addressed multiple stability and disturbance components in one experiment (Donohue et al. 2016). This likely results from methodological challenges in measuring multiple variables across an entire ecosystem. Given that the ecosystem services concept encompasses functions derived from almost all levels of an ecosystem, the current empirical framework on which stability-promoting policies can be based on seems insufficient. What Donohue et al. (2016) may be alluding to then, in order to better answer the question, is the harmonisation of the ecosystem multifunctionality and stability paradigms. This harmonisation could exist in the intersection of biodiversity, ecosystem multifunctionality (Tilman 1997; Hector et al. 1999; Diaz and Cabido 2001) and stability, an area that has recently gained important traction (Mouchet et al. 2010; Carmona et al. 2016).

Although the diversity-stability debate remains, at present, unanswered, both classical and recent reviews have consistently called for increased field-based data to be collected from across trophic levels and beyond species richness assessments (Hooper et al. 2005; Donohue et al. 2016; Eduardo 2016; Nikisianis and Stamou 2016). McCann (2000) critically assessed the diversity-stability topic concluding that stability likely originates from the high level of interconnectedness between trophic levels whereas instability on the other hand results from species loss which reduces interconnectedness (for further developments of this idea see Kadoya and McCann 2015; Tunney et al. 2012). Large scale experiments have also revealed that environmental conditions and grassland diversity may not be the most important contributors to multifunctionality and aboveground vegetation biomass production may not be the most important measure of functionality but that individual trophic levels may contribute more than others to particular functions (Soliveres et al. 2016b). It appears then that inter-trophic relationships contribute importantly to stability. This is consistent with theses highlighting that ecosystem functions are mediated by complex aboveground and belowground biota linkages (Wardle et al. 2004; Gossner et al. 2016). However, the mechanisms and their

magnitudes and directions involved in promoting ecosystem connectedness and, by extension, stability and sustainability remain unknown.

The rate at which multifunctionality is lost varies geographically, between ecosystem types, across trophic levels (Lefcheck et al. 2015) and land use intensities (Allan et al. 1997; Gossner et al. 2016). However, many of these ecosystem stability and multifunctionality studies have been conducted in grassland ecosystems (Lefcheck et al. 2015; Donohue et al. 2016) which are both economically and socially important and globally threatened, principally by land transformation and degradation through eutrophication, overgrazing, and herbivore or fire exclusion (Cremene et al. 2005; Wright and Wimberly 2013; Hautier et al. 2014; Parr et al. 2014; Hautier et al. 2015). If ecosystem functioning is a key component of ecosystem sustainability, then the underlying mechanisms maintaining and promoting functionality should be studied in greater detail and incorporated into the ecosystem services discipline. In little over a decade there has been substantial development in the volume of literature addressing the diversity-stability debate (52 studies identified in 2007 by Ives and Carpenter (2007); 354 studies identified in 2016 by Donohue et al. 2016). We believe that a systematic map (a broad overview of evidence relating to a broad but important policy or management question) identifying the drivers of the various measurements of ecosystem stability in grassland ecosystems from across the globe could help identify solutions to a broad and challenging topic. A systematic map to capitalise on this rapid growth and identify future research trajectories for the ecological stability literature will make important contributions to both pure and applied ecologists and land managers working to maintain reliable ecosystem functioning through space and time.

This systematic map could also be incorporated into current ecosystem assessment protocols by encouraging increased focus towards relevant drivers of ecosystem stability — a potentially valuable tool for assessing policy effectiveness, implementation success, and ecosystem management sustainability (Mace et al. 2012). Areas needing deeper research and areas where systematic reviews and meta-analyses can be carried out will also be highlighted through this systematic map.

1.2 Stakeholder engagement

The scope and focus of the systematic map were broadly established by the review team and then refined following stakeholder input. Stakeholders were engaged via an online Google Forms survey. Approximately 60 invitations were sent out via email to potential stakeholders with 22 responses received. The majority of the respondents identified as academics (68.2%) with the next biggest group identifying as directly influencing local or national policy and governance (18.2%). Most stakeholders were South African (41.01%), North American (31.81%), and European (18.18%) with one Brazilian respondent. Stakeholders provided key input into search string development and contributed key articles which were incorporated into the test list. Although we could have recieved a greater number of responses the demographic was helpful to guide the question development. Several helpful suggestions on the systematic map presentation were also provided (see the Supplementary materials of Demmer et al. (2018) for the individual and summarised responses).

1.3 Objectives of the systematic map

The primary objective of this systematic map was to map the current relationship patterns related to the biotic and abiotic drivers of grassland ecosystem stability from across trophic

levels. Given the breadth of the topic, a primary research publication search (which yielded in excess of 100 000 publications) was not feasible. Data for this map were therefore sourced from literature reviews and meta-analyses addressing natural, conserved, and agricultural grasslands from across the globe. The outputs of this systematic map consist of a graphical overview of the "state of the art" of the grassland stability discipline, an exploration of the consensus within the academic community of the existence and direction of common driver-outcome relationships together with a narrative synthesis assessing these consensuses in relation to key experimental and observational evidences.

There have also been recent calls that solutions to the problem of decreasing ecosystem sustainability should be based on ideas synthesised from the pure ecology discipline and then implemented into society at large (Donohue et al. 2016; Manning et al. 2018). This study thus, secondarily aims to identify areas where ecologists and stakeholders may enter into relationships to identify and develop future questions and solutions which can be applied to policy revisions and development.

1.3.1 Primary question

What evidence is available on the drivers of grassland ecosystem stability across a range of outcome measurements?

Components of the primary question

Population/subject: Experimentally manipulated, undisturbed, conserved, or extensively managed grasslands. Depending on the focus of the review, references to studies within the savanna biome were also included. Studies where the grassland had been structurally altered anthropogenically into a monocrop or had experienced dramatic urbanisation were not included.

Intervention/Exposure: Potential drivers of grassland ecosystem stability largely acknowledged in the ecological literature. These included positive drivers such as diversity and food web connectedness but also negative drivers such as invasions or climatic variabilities.

Outcome: Measures of grassland ecosystem stability largely acknowledged in the ecological literature. Commonly used measurements included temporal coefficients of variation, changes in vegetation composition and return times to a pre-disturbance state.

1.4 Methods

1.4.1 Searches

Search terms

The search term consisted of three parts each pertaining to the three aspects of the primary question; population, driver (which includes both intervention and comparator terms) and outcome. Search terms were selected based on both stakeholder consultation together with the consultation of key studies to identify terminology relevant to the primary question. These studies are outlined below. The population search consisted of synonyms referring to 'grassland' from across the globe. This list was generated by extracting commonly occurring terms in the International Vegetation Classification Divisions used to describe grassland regions (Dixon et al. 2014) together with stakeholder input. Drivers of ecosystem stability comprising the intervention component of the primary question were selected from terms suggested as

important from key diversity-stability debate reviews (McCann 2000; Ives and Carpenter 2007; Donohue et al. 2016) together with articles and suggestions from the stakeholder community. The terms comprising the outcome search string component were selected from a thematic review (Ives and Carpenter 2007) and a terminology inventory article (Grimm and Wissel 1997) together with articles and suggestions from the stakeholder community.

The search was based on three groups of search terms, the grassland synonyms (population), the contributors to stability (driver), and the stability measurements (outcome). Search terms within each question component were combined using the Boolean "OR" operator. Each question component was then combined using the "AND" operator. Wildcards (*/$) were used to return multiple prefixes and suffixes.

Population: *grass* OR prairie* OR meadow* OR rangeland* OR steppe OR veld* OR pasture* OR pampa* OR heath* OR tagia* OR campo* OR llano* OR tundra OR lawn

Driver: richness OR *synchron* OR turnover OR divers* OR *function* OR process* OR product* OR BEF OR complexit* OR interact* OR *connect* OR web OR network OR trophic OR invasion* graz* OR *herbivor* OR fire OR drought OR precipitation OR rain* OR fertili* OR land use OR perturb* OR disturb* OR spatial varia* OR temporal varia* OR spatio-temporal varia* OR pulse*

Outcome: stabl* OR unstabl* OR *stabilit* OR *sustain* OR chao* OR invasibilit* OR coefficient of varia* OR resist* OR return* OR Holling* OR resili* OR alternat* OR recover* OR collapse* OR *equilibrium OR transition

No time or document type restrictions were applied to database searches. Only the English language was used to search within the databases.

Publication database

The ISI Web of Science Core Collection was queried on 27 March 2019. We then filtered out all articles returned by the query which were not of the "review" type.

Grey literature

As this review is focussed on identifying relevant review studies, no grey literature searches were conducted.

Assessing the specificity and sensitivity of the search

Comprehensiveness tests of the search terms were assessed using ISI Web of Science (see the Supplementary materials of Demmer et al. (2018) for the results of the comprehensiveness tests). This assessment was conducted across all kinds of articles, not restricted to review articles. Each proposed population search term was queried together with AND (*stabl* OR *stability*). The full population search string together with AND (*stabl* OR *stability*) was then queried together with each driver term. Finally, the full population and driver search strings were queried together with each stability outcome search term. Each term's specificity was assessed by recording the number of hits returned for each term and the proportion of relevant results (out of 50 citations screened at title level). To give an indication of each term's (and each full string's) sensitivity the number of test list articles returned was also recorded. The test list (see the Supplementary materials of Demmer et al. 2018) was developed based both on contributions from stakeholders via the survey and from the review team. All

stakeholder and review team test article suggestions were then considered, and a final list was developed which covered a range of topics relating to the components of the primary question as well as being drawn from various key journals and authors. The final search term included all articles in the test list.

Article retrieval strategy

All articles obtained during this systematic map were stored in bibliographic files. All bibliographic data were then loaded into EndNote X8, compiled into one library and duplicate references were removed. This library was then exported and uploaded to CADIMA (`https://www.cadima.info/`). Inclusion/exclusion criteria were then applied. Publications for which the full text was not accessible were excluded as these files were needed to both accurately assess the study validity and identify driver-outcome relationships.

1.4.2 Article screening and study eligibility criteria

Article screening

Search results were screened by the same individual over two stages: title and abstract together, and full text. Articles included at title and abstract level were then screened at the full text level.

Eligibility criteria

Each study had to fulfil the following criteria to be included in the map:

Relevant subjects Grasslands across the globe. Grasslands may include any extensively managed, conserved, undisturbed or disturbed region which is primarily dominated by grasses and forbs, shrubs, crusts, and or succulents. Studies concerning dramatic anthropogenic influence (e.g. ecological restoration, intensive agricultural practices) and studies conducted in natural systems were included. However, studies where the grassland had been structurally altered anthropogenically into a monocrop or had experienced dramatic urbanisation were not included. As this map was focussed on grasslands, studies conducted within savanna or forest habitats were not targeted. However, those which address the dynamics between grassland and wooded states were included. No studies conducted in fresh (e.g. wetlands, deltas, marshes) or marine (seagrass meadows, beaches) aquatic systems were included. However, studies conducted in grasslands occurring along the boundaries of any of these systems were included. Studies documenting "paleo-grasslands" were not included.

Relevant stability drivers Drivers were any measure of diversity (e.g. alpha, beta, gamma, richness), climate (e.g. precipitation, fire, drought, temperature), disturbance (e.g. grazing, fertilisation), trophic level complexity (number of levels, number of nodes, network asymmetry, network nestedness).

Relevant types of outcomes There must have been a measurement of stability reported in the review. These included variability (or its inverse), coefficient of variation, network stability, rates of ecosystem functioning, persistence following disturbance, return time until reaching a pre-disturbance state, transitions into alternate stable states or temporal fluctuations. Studies that alluded to their results being important in the diversity-stability debate without actively referring to other studies were not included in the map.

Relevant types of study Opinion, synthesis, commentary, and narrative or quantitative review articles which were found to be relevant were also included in the database and were coded

accordingly for easier future reference.

Language Only studies published in English were included during screening.

Date No date restrictions were applied.

1.4.3 Study validity assessment

Because this study considered only review publications, assessing the methodological validity was not possible as few review articles report their methods accurately enough in order to be repeated.

1.4.4 Data coding strategy

Following full-text screening, included review publications were reviewed to identify references to grassland stability measurements. Where a review made mention of a particular ecosystem process being associated with another ecosystem process, the relationship was recorded. Based on the phrasing by the original authors we inferred the driver and the outcome of the relationship. In some cases where there were "gradients" or subcategories of a particular driver distinctions between these levels were incorporated based on the wording of the original authors. Two important distinctions that were drawn were 1) the difference between plant invasions and woody plant expansion and 2) presence of herbivores (whether natural or well managed agricultural herds) and poorly managed (perhaps in the form of overstocking, prolonged grazing, or where there was excessive selective grazing by certain animal types) which was classified as "Heavy grazing". Furthermore, we recorded whether the driver was believed by the review publication authors(s) to have a positive (1), negative (0) or null (0.5) effect on the outcome. This was done to determine the consensus among academic researchers of the direction of a given relationship.

1.4.5 Results presentation and statistical analysis

A total of 2383 review publication records were identified through database searching. No duplicates were identified. During title and abstract screening, 1728 records were excluded. Of the remaining 655 records screened at the full text level, 330 were excluded either because the full text file was not accessible or because the review publication did not meet the inclusion criteria. A total of 325 review publications were subsequently assessed to identify grassland ecosystem stability driver-outcome relationships.

Following relationship identification, drivers and outcomes were categorised in a hierarchical manner to aid relationship visualisation and interpretation by the reader. All plots and analyses were conducted in R version 3.6.1 (R Core Team 2019). The dataset was then summarised to determine the number of times each relationship was identified. The resulting dataset was then presented visually as a Circos plot (Krzywinski et al. 2009) generated using the `chord_diagram` function from the `circlize` package (Gu et al. 2014). Only relationships where three or more records were identified were included in this plot as the function was not able to produce the plot based on the entire dataset due to the number of connections required.

Where several records of a given relationship were identified, the probability that the relationship would be positive or negative was modelled using generalised linear models via the `glm` function from the `stats` package. Residuals were modelled using binomial distributions and logit link functions were used to ensure proportional responses. A separate model was conducted for each driver-outcome relationship. For all analyses the probability was

distributed by the intercept only. Significance was determined at $\alpha = 0.05$ and indicates the consensus difference to $p(\mathrm{x}) = 0.5$ (no consensus among academic researchers).

1.5 Results

A total of 2649 driver-outcome relationships were identified of which 1681 were unique. Many of these relationships were only identified once or twice with only 168 relationships reported in the literature three or more times. These 168 relationships are summarised in Figure 1.1. Aboveground-aboveground relationships made up 61.23 % of the dataset, 22.69% of the relationships occurred between aboveground-belowground or belowground-aboveground ecosystem properties with the remainder occurring between aboveground-both or belowground-both ecosystem properties.

Plant diversity, fire, plant invasions, heavy grazing and herbivory were found to be the most common ecosystem stability drivers. Plant abundance (measures of the total amount of plant material, e.g. biomass, cover, density, etc.), plant diversity, plant invasion and woody plant abundance were the most commonly reported stability outcome categories. Plant diversity (number of unique associations with other processes = 64), fire (57), plant invader abundance (53), agriculture (44), heavy grazing (43), herbivore abundance (39), fertilisation (39), herbivory (38), temperature (37), plant abundance (36), nitrogen deposition (34), woody plant abundance (34) and physical soil disturbance (33) were the ecosystem stability drivers which drove the most number of ecosystem stability outcome measurements. The ecosystem stability outcomes that were associated with the most ecosystem stability drivers were plant invader abundance (76), plant diversity (96), plant abundance (63), restoration (39), plant compositional shifts (38) and ecosystem functioning (32).

The consensus of the direction of the relationships which were reported by 10 or more review publications was then assessed. The strength of these relationships are presented in Figure 1.2 and described in the remainder of this paragraph. Plant diversity was reported to be negatively affected by nutrient addition ($Z = -2.101$, $p = 0.0357$). However, invasive plant abundance ($Z = -1.858$, $p = 0.0631$) and herbivory ($Z = 1.754$, $p = 0.0795$) were often reported to have inconsistent effects on plant diversity. Plant diversity was often reported to have positive effects on ecosystem functioning ($Z = 2.662$, $p = 0.0078$) whilst inconsistent reportings of plant diversity ($Z = -1.700$, $p = 0.0892$) and fire ($Z = 0.288$, $p = 0.7731$) effects on invasive plant abundance resulted in no consensus being drawn for these relationships. Both heavy grazing levels ($Z = -2.296$, $p = 0.0217$) and fire ($Z = -1.609$, $p = 0.0377$) were consistently reported to reduce plant abundance whilst plant abundance was commonly reported to be promoted by plant diversity ($Z = 3.313$, $p = 0.0009$). Heavy grazing was consistently associated with rangeland degradation ($Z = 2.472$, $p = 0.0134$). Stability was commonly reported to increase as plant diversity ($Z = 3.037$, $p = 0.0024$) or species asynchrony increased ($Z = 2.944$, $p = 0.0424$). Finally, woody plant abundance was often negatively associated with both fire ($Z = -3.178$, $p = 0.0019$) and herbivory ($Z = -2039$, $p = 0.0414$).

1.6 Discussion

The results of this literature review highlight the overwhelming complexity of ecological interactions within the grassland biome. Many of these complexities link both above- and belowground biota and processes. Several earlier reviews have highlighted the existence of

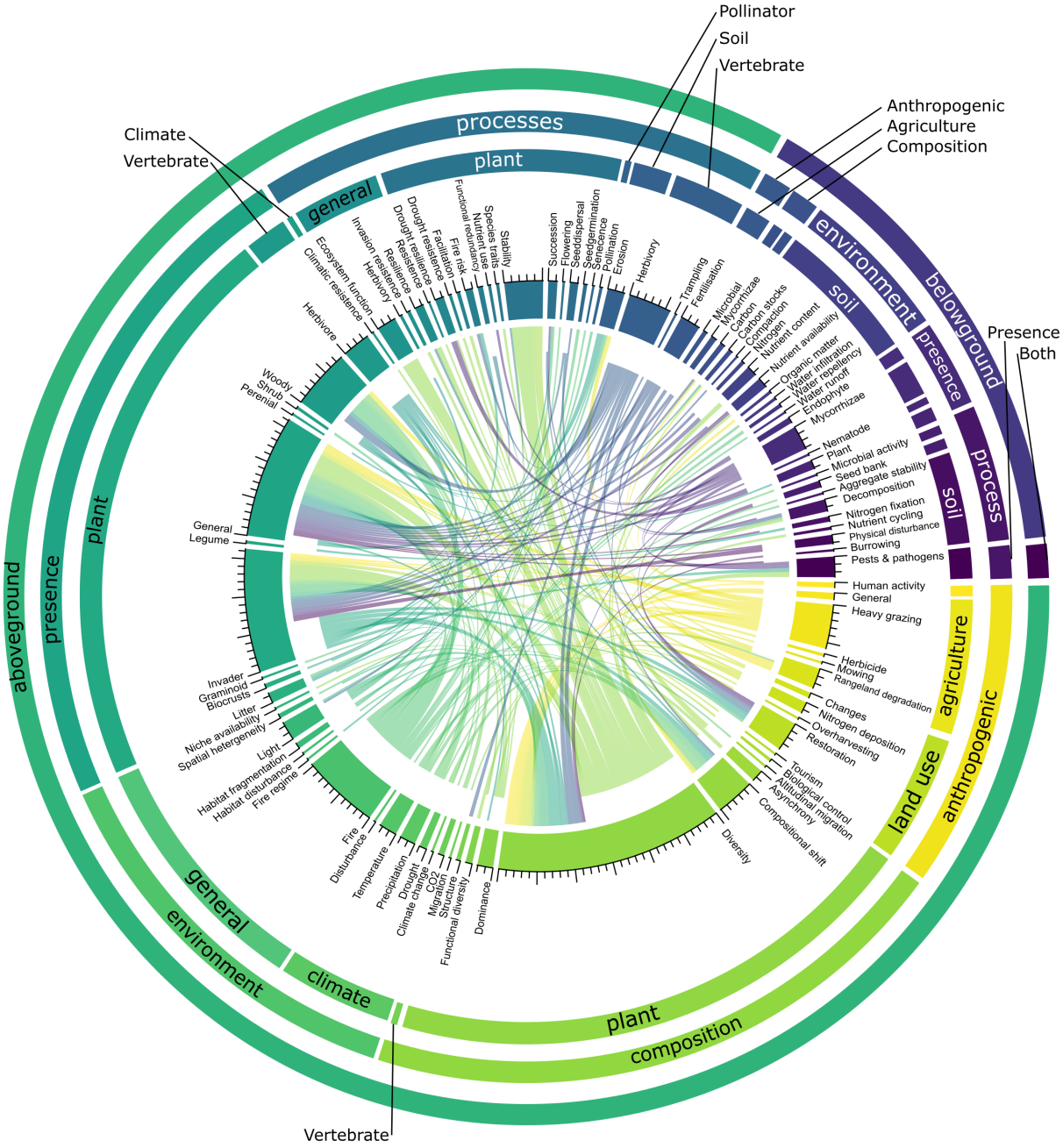

Figure 1.1: An overview of the driver-outcome relationships relating to grassland ecosystem stability identified from published literature reviews. Ninety-two aspects of the ecosystem were identified in the literature more than three times and are arranged circularly. The number of times an aspect was identified is represented by the width of the thick, inner-most coloured region (minor ticks = 10 identifications, major ticks = 50 identifications). Driver-outcome relationships are represented by chords. Chords beginning away from the inner-most circumference represent stability drivers and chords ending on the inner-most circumference represent stability outcomes. Aspects are categorised hierarchically from the outer to the inner rings surrounding the main plot by labelled arcs.

these relationships (Bardgett and Wardle 2003; Wardle et al. 2004), however, this review provides a more quantitative overview of the distribution of these relations. We also found that aboveground-aboveground relationships were 2.7 times more likely to be reported on than

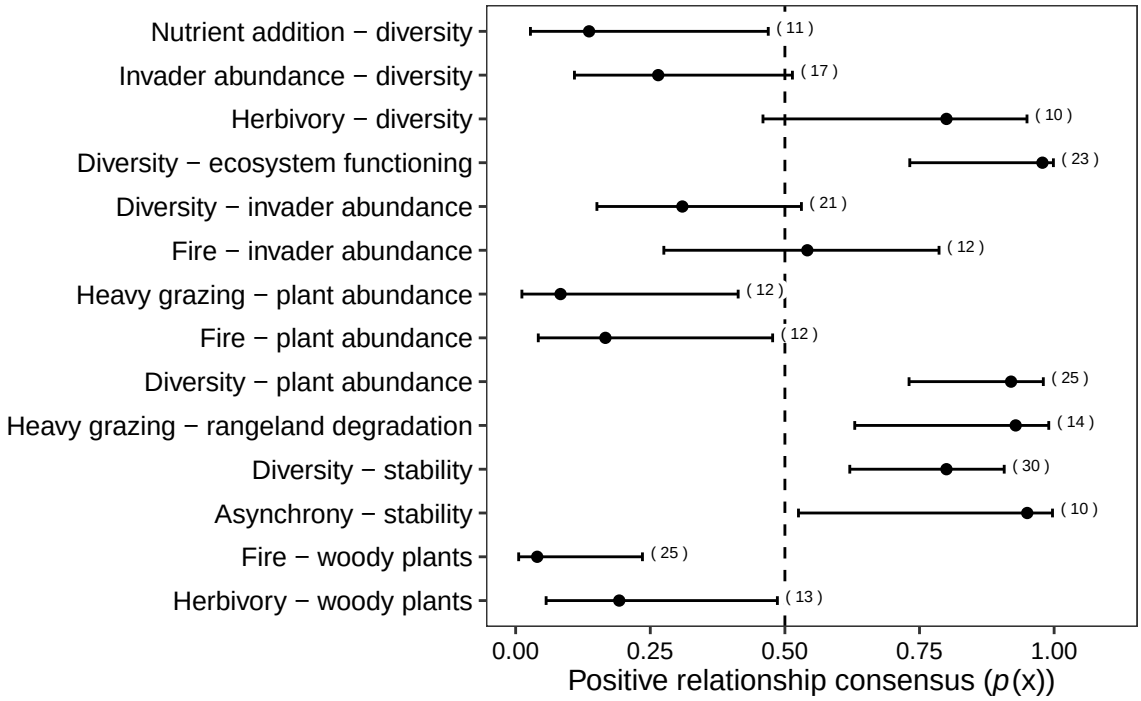

Figure 1.2: Academic consensus of negative ($p(x) = 0$) or positive ($p(x) = 1$) relationships existing between grassland ecosystem stability drivers (left of the "–") and their associated outcomes (right of the "–") based on indications in literature review publications. The dotted line represents the null effect line ($p(x) = 0.5$). Values to the left and right of this line represent negative and positive relationship consensus, respectively. Confidence intervals which overlap the dotted line indicate that there is inconsistency in the direction of the reported relationship. Numbers in parentheses indicate the number of literature review publications reported the relationship.

relationships between aboveground and belowground properties, something that is potentially concerning especially given that no natural aboveground or belowground processes were consistently reported as being important to some aspect of grassland stability. An encouragement here is that the plant-soil feedbacks discipline appears to be gaining traction with recent articles outlining the purpose of this discipline as well as how to conduct effective research (Pernilla Brinkman et al. 2010; Lekberg et al. 2018; Rinella and Reinhart 2018).

The remaining discussion attempts to unpack the mechanisms likely underpinning the most commonly reported stability driver-outcome relationships. We also attempt to highlight where strong consensus lies as well as why, despite being reported many times, little consensus exists for the direction of other commonly reported relationships.

1.6.1 Heavy grazing and woody encroachment

We found that there is a strong negative consensus relating to the impact of heavy grazing on plant productivity and rangeland condition. Poor grazing management in the form of overstocking negatively affect grasslands across the globe by causing desertification, reduced forage quality, soil erosion and reduced water quality, and woody plant encroachment (Otterman 1974; Sonneveld et al. 2005; Liu et al. 2013; Stevens et al. 2016; Middleton 2018; Oliva et al. 2019). Pastoralists understand the socio-ecological and socio-economic consequences of reduced rangeland condition (Reid et al. 2014; Kimiti et al. 2016; Sala et al.

2017) but the risks of overgrazing are especially felt in arid regions (Liu et al. 2013; Dlamini et al. 2016) and are often exacerbated under climate change (Liu et al. 2013). However, this does not mean that the effects of overgrazing are restricted only to arid regions. Mesic regions may be equally negatively affected by poor grazing management regimes (Scott-Shaw and Morris 2015) but heavy grazing's effects taking the form of species compositional (**Hayes2003**; **Morris2019**) as well as vegetation structure (**Cingolani2003**) changes in vegetation rather than losses of vegetation altogether.

We found that academics consistently linked woody plant encroachment with unsustainably high levels of grazing. Woody plant encroachment rapidly transforms ecosystem structure, diversity and functioning (Stevens et al. 2016). There is substantial research available highlighting the major concerns pertaining to increasing bush encroachment levels in relation to biodiversity and ecosystem and agricultural functioning (Eldridge et al. 2011; Ratajczak et al. 2012; Alofs and Fowler 2013; Anadon et al. 2014). Whilst bush encroachment may negatively impact some grassland ecosystems, arid regions appear to benefit from woody plant encroachment (Eldridge and Soliveres 2014; Soliveres et al. 2014; Mureva et al. 2018). Interestingly, there have been recent attempts (such as the efforts of the Bonn Challenge - www.bonnchallenge.org) to further encourage the expansion of woody plants into regions classified as degraded rangelands (as defined by the World Resources Institute (WRI) - www.wri.org/resources/maps/atlas-forest-and-landscape-restoration-opportunities) in an attempt to sequester carbon and offset forest habitat losses in the higher latitudes. Although this approach seems benefical some argue that the effectiveness of these projects would be small (Arora and Montenegro 2011) if anything (Smith et al. 2016b). Bond et al. (2019) have taken this discussion further and strongly objected to this kind of afforestation which they believe is based on a poor understanding of carbon sequestration processes. Bond et al. (2019) also highlighted the important roles grasslands in their intact state contribute to ecosystem functioning. The fact that some very well managed and preserved grasslands (for example the Kruger National Park and the Serengetti National Park) are classified by the WRI as degraded rangelands emphasises how poor an understanding these policy makers have of ecosystem quality (Bond et al. 2019). Furthermore, grasslands are capable of sequestering huge quantities of carbon whilst forested or woody encroached areas sequester carbon poorly (Coetsee et al. 2013; Dass et al. 2018). Rather than undertacking massive tree planting campaigns to "restore" "degraded" grasslands, simply reinstating proper grazing management could enable grasslands to sequester impressive amounts of carbon (Conant and Paustian 2002). This could also and promote other ecosystem processes through the suggestion (although not complete consensus) among most academics that herbivory promotes plant diversity.

Although the woody plant encroachment problem is gaining global relevance, there are many options available to combat the spread of woody plants. Ding et al. (2019) examined the recovery of several grassland ecosystem properties in response to several different woody plant encroachment control methods. They found that grassland ecosystem responses vary greatly depending on the environmental and management context. However, they also cautioned that there may be some circumstances (hotter and drier climates which could be experienced in the future) where grasslands could even benefit from woody encroachment. Interestingly, Ding et al. (2019) (citing Parr and Andersen 2006) cautioned against the broadscale application of fire in response to woody encroachment despite fire generally being considered beneficial for biodiversity. We take this consideration seriously and caution that applying fire to control woody plant encroachment should be carefully considered despite there being strong consensus among academics that fire does control woody plant encroachment.

1.6.2 Land use

We were surprised to find relatively little commentary exploring land use change impacts on grassland ecosystem functioning or stability. This was especially because of the impressive effect that changes in land use type and intensity can have on both species diversity and ecosystem functioning (Foley et al. 2005; Allan et al. 2015). Recently Blüthgen et al. (2016) explored this idea by investigating the importance of diversity and asynchrony changes across different land use types. They attributed reduced stability under increased land use intensity to reduced species asynchrony rather than reduced diversity. Other studies have also identified functional diversity, community composition and plant trait shifts as more important predictors than species level variables when assessing land use change impacts on ecosystem functioning (Vandewalle et al. 2010; Rader et al. 2014; Allan et al. 2015; Mumme et al. 2015).

Our concern is that despite there being some work exploring the effects of land use change on biodiversity, ecosystem functioning and stability, we found a much greater focus on other ecosystem properties such as plant invasions, fire, and woody plant encroachment. Similarly, Titeux et al. (2016) described the exponential growth which has taken place in climate change research whilst highlighting that almost no expansion of our understanding of land use and land-cover changes has taken place in recent decades. Given the immediate and direct threat of land use change on biodiversity and its associated ecosystem properties, we strongly encourage future research into this field.

1.6.3 Top-down and bottom-up

Our review brought to light apparent inconsistencies relating to plant diversity being controlled by plant invasions and herbivory. Considering these two processes in combination with plant diversity's negative response to fertilisation suggests that there is a consensus within the literature that plant diversity is a function of resource availability and competition. We identified a weak, non-significant consensus that without management processes acting on the ecosystem (e.g. in the form of herbivory or fire), plant communities have the potential to succumb to invasion. However, the inconsistencies around this suggest there are likely triggers which initiate the compositional shift to an invaded state (Tilman 1997).

Nutrient addition and herbivory were the two other external processes commonly thought to be involved in shifting plant diversity possibly through their impacts on resource availability within the environment in combination with the competitive ability of individual plant species (Tilman 1982). Alterations to plant resource availability can occur through bottom-up processes of nutrient deposition which promotes aboveground productivity and reduces light availability thereby excluding uncompetitive species (Hautier et al. 2009). However, recent key work has shown that top-down processes such as herbivory or mowing (both as means of aboveground defoliation) could be used as a general solution to this problem by increasing light availability at ground level (Yang et al. 2012; Borer et al. 2014a) and reducing plant dominance (Mortensen et al. 2018) to allow subordinate or uncompetitive species to coexist. Given the tendency in our findings towards increased and decreased diversity following herbivory and nutrient addition, respectively, we emphasise the dissemination of these findings into policy development.

1.6.4 Confusion around fire

Whilst fire was consistently reported to control woody plant encroachment, the benefits of fire's effects on plant invasions (the increased dominance of alien plants within region)

appeared to be less well agreed upon by the scientific community. Fire is known to both prevent (Gordijn et al. 2018) and also promote (McKenzie and Tinker 2012) plant compositional change in grasslands. The negative connotations between fire and plant invasions could perhaps be related to the plant composition. As greater proportional abundance of grass within a sward promotes fire spread and intensity (Wragg et al. 2018), invasions that alter fire regimes (through reduced grass cover, for instance) are often reported to initiate positive plant invasion feedback cycles. These cycles result in the exclusion of native fire tolerant plants in place of competitive exotics (Pausas and Keeley 2014; Padullés Cubino et al. 2018). Another positive feedback cycle could occur under circumstances where the invasive plants are fire tolerant grasses. Increased fire application to control the invasion may have the opposite effect of excluding the native fire sensitive plant species and promoting the dominance of the exotic fire tolerant species (D'Antonio and Vitousek 1992; Fisher et al. 2009).

Varying opinions pertaining to the use of fire and plant invasions could also be because the direction of fire's effects on plant invasions are dependent on the prevailing environmental conditions. Fire may promote plant invasions in regions where fire, although integral to the community's functioning and persistence (such as Mediterranean grasslands), occurs at relatively lower frequencies. Alterations to these fire regimes may impact the community's resilience and predispose to plant invasions (Kruger 1983; van Wilgen et al. 1994; Diaz-Delgado et al. 2002; Colombaroli et al. 2007). Increased plant invasions in regions where fire occurs at lower frequencies could be inevitable given that high fire intensity can create gaps in these regions (Keeley et al. 2003; Santana et al. 2014). Applying fire to Mediterranean regions, especially for managing invasive plants, therefore needs important consideration (Holmes et al. 2000).

On the other hand, both paleoecological and current rangeland management paradigms do agree that, at least for the majority of temperate and mesic grasslands, fire and grazing have both shaped grassland vegetation structure and functioning and that they work together to promote and stabilise agricultural productivity (Van Langevelde et al. 2003; Bond and Keeley 2005; Parr et al. 2014). Applied together, there is a growing belief that fire and herbivory can encourage both spatial and temporal heterogeneity thereby increasing biodiversity and stability in rangelands (McGranahan et al. 2012; McGranahan et al. 2016; McGranahan et al. 2018).

1.6.5 Diversity, stability and ecosystem functioning

The relationship between diversity and ecosystem productivity has been a topic of debate for decades. Numerous empirical attempts have been made to understand this relationship ranging from strong positive effects to weak, null or even negative influences of diversity on stability. Diversity-productivity relationships may be linear, non-linear or non-existent (Tilman et al. 1996; Hector et al. 1999; Adler et al. 2011) with the relationship likely being multivariate (Adler et al. 2011) and a function of environmental conditions (Grace et al. 2007). There is evidence that this relationship is capable of persisting through disturbances (Tilman and Downing 1994; Craven et al. 2016). Thus there seems to be substantial uncertainty relating to the diversity-productivity debate, however, we found the opposite occurring in review literature with a strong consensus that diversity promotes grassland productivity. Despite the lack of a direct relationship detected in field studies, incorporating multiple ecosystem properties and processes can generate an holistic overview of how diversity and other ecosystem properties interact to control productivity (Grace et al. 2016). Importantly, even in those areas where diversity is associated with productivity, diversity often accounts for only a small proportion of the variation (Adler et al. 2011). Therefore given the complexity of

the relationship between diversity and productivity, we therefore caution against broad statements such as "diversity promotes plant productivity" (Lambers et al. 2004).

Interestingly, our review identified that fire is an inhibitor of plant abundance. Given that fire is often viewed as a herbivore (Bond and Keeley 2005), it is understandable that fire reduces plant aboveground biomass. However, that need not be viewed negatively as fire can have positive effects on belowground productivity (Reich et al. 2001). A recent meta-analysis revealed that long-term fire regimes do play an important role in soil nutrient dynamics with productivity declines following fire being attributed to soil nitrogen losses (Pellegrini et al. 2018). If productivity is the chosen measure of ecosystem functioning and stability, then perhaps fire is a poor management tool. We do, however, stress the importance of defoliation of the grassy vegetation component of ecosystems (whether by mowing, herbivory or fire) in order to maintain ecosystem diversity and functioning and reducing dominance, all of which are associated with increased plant abundance (Fynn et al. 2011; Borer et al. 2014a; Lepš 2014; Hautier et al. 2018).

There was another strong consensus regarding the relationship between plant diversity and stability. Chalcraft (2013) showed that across many experimental studies, biodiversity does have a positive effect on both ecosystem and population stability. This Chalcraft (2013) and others (Loreau and de Mazancourt 2008; Hector et al. 2010; Wilcox et al. 2017a) have attributed to species asynchrony in either theoretical or experimental contexts. We find this strong consensus concerning the relationship between asynchrony and stability present in review publications (and thereby becoming cemented into ecological theory) encouraging especially given that the asynchrony concept has only begun to be experimentally tested relatively recently.

1.6.6 Future directions

This review provides a novel and detailed overview of the current consensus of the drivers of grassland ecosystem stability and the associated outcomes. Our approach has revealed patterns that have formed into paradigms over recent decades. For the most part, we have found strong agreement among researchers relating to several recurring relationships. We believe that these topics should rapidly be incorporated into grassland conservation and management policies. However, despite good discussion within the scientific community, there are still outstanding issues of how plant invasions and defoliation relate to other ecosystem processes. We also acknowledge the concerning absence of opinion on land use change and climate related drivers and outcomes in relation to grassland ecosystem stability. Both these areas could be deserving of proportionately greater research in the near future.

We have revealed the breadth and depth of the diversity-stability-ecosystem functioning discipline showing that it touches all parts of our globe and expands across trophic levels. Given the popularity of some aspects of the discipline in review publications, we believe that there are definite possibilities for more refined and focused systematic maps and subsequent systematic reviews and meta-analyses of primary evidence which could unpack information at more relevant scales.

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Ethics approval and consent to participate

Ethics approval for this study was granted by the University of KwaZulu-Natal's Humanities & Social Sciences Research Ethics Committee (approval number HSS/1620/018M).

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Chapter 2

Species losses following persistent nutrient addition improves grassland rain use efficiency stability in response to temperature variation

Abstract

Future climatic projections suggest greater and more variable high temperature extremes which will have important implications for grassland species dynamics and productivity. Species diversity likely influences changes in grassland stability following disturbances such as climatic stress or eutrophication. However, when such disturbances co-occur grassland responses can be unpredictable owing to shifts in competitive interactions between species. Understanding how plants exposed to high temperatures (which negatively influences the ability of plants to take up soil nutrients and water) together with changes in soil nutrient status may provide important insight for grassland management. This study aimed to explore how productivity magnitude, variability, and stability of Control (characterised by high species diversity and dissimilarity, and more even abundance distribution across species) and nutrient enriched (characterised by low species diversity and dissimilarity, and less even abundance distribution across species) grasslands responded to climatic stress both annually and over three-year periods. We utilised rain use efficiency (RUE) data collected from a long term, *in situ* grassland experiment to understand how the temporal stability of RUE and its constituents (temporal mean and temporal standard deviation (SD)) changed across mean maximum temperature and maximum temperature SD. Maximum temperature SD was a better predictor of RUE metrics than mean maximum temperature. Mean RUE and RUE SD both increased as maximum temperature SD increased, but RUE SD increased more rapidly in Control grasslands than in nutrient enriched grasslands. Control grasslands, therefore, became destabilised in response to variation in temperature stress. Greater RUE stability in nutrient enriched grasslands may have resulted from dominance by particular grass species, perhaps with larger root systems and faster growth rate making them more resistant to water-related stress than species of other functional groups. Lower RUE stability in Control grasslands could be indicative of a plant community capable of responding dynamically to climatic variability. Control grasslands could then be more resilient to several co-occuring disturbances.

Keywords: *biodiversity-stability relationships* • *eutrophication* • *global change* • *resilience* •

high temperature stress • Ukulinga Research Farm

2.1 Introduction

Anthropogenic and climatic factors are important influencers of grassland stability and impact the persistence of grassland plant communities (Hooper et al. 2012; Hautier et al. 2015; Isbell et al. 2017). Current projections suggest that future climates will differ markedly from today's, resulting in substantial losses of habitat ranges for both animal and plant species (Warren et al. 2018). These altered climatic conditions are likely to have important effects on grassland functioning (Fay et al. 2008) and stability (the ability of an ecosystem to consistently supply a function such as biomass production through time under varying conditions) with these impacts being magnified through species composition changes (Bloor and Bardgett 2012; Hooper et al. 2012; Prieto et al. 2015).

Species losses in grasslands may occur due to varying characteristics among species within the species pool which dictate their abilities to persist through climatic variations (Harrison et al. 2015; Smith et al. 2016a). These are likely dictated by plant responses to climatic stressors which take place at the gene expression level (Travers et al. 2010). Individual plant-level resistance to climatic variation is primarily a function of plant physiology whereas grassland community responses relate to resource availability and variation in the competitive abilities of species inhabiting the community. For example, belowground nutrient release promotes aboveground biomass productivity which excludes uncompetitive and unproductive species through reduced light availability (Farrer and Suding 2016; Harpole et al. 2017).

These community destabilisation processes do not often affect grassland communities in isolation. For example, increased water availability and anthropogenic eutrophication can have additive effects on grassland biomass production (DeMalach et al. 2017).
Nutrient-environment interactions also occur along elevation gradients with eutrophication impacts being more strongly associated with climatic variables (such as extreme temperatures) as grassland altitude increases (Humbert et al. 2016). This is possibly because of greater co-limitation of water and soil nutrients in these higher altitude grasslands (Eskelinen and Harrison 2015). It has also been reported that defoliation can aid drought-stressed grasslands by minimising water losses through evapotranspiration (Luo et al. 2012).

Across the globe grassland production and functioning is strongly dependent on rainfall (Snyman and Fouché 1993; Knapp et al. 2001; Swemmer et al. 2007; Bai et al. 2008; Fay et al. 2008; Petrie et al. 2015; Dudney et al. 2017) with mesic South African grassland productivity being controlled by within season precipitation patterns (Knapp et al. 2006). Furthermore, without sufficient precipitation, grassland productivity is often limited, regardless of the available soil nutrients (Knapp et al. 2001). Therefore, altering the factors controlling the rainfall use efficiency (RUE, the amount of biomass produced per unit of rainfall - $g \cdot mm^{-1}$) of grassland plants (such as soil and plant moisture dynamics and photosynthesis, Fay et al. 2003) would impact the community's rate of production rather than the community's net production. Understanding the rate of grassland production as a function of rainfall rather than aboveground net primary production alone may be a better measure of grassland functionality.

Precipitation patterns and factors which control water availability are therefore important controllers of grassland functioning. However, plants can be further impacted by combined climatic stressors. For example, De Boeck et al. (2016) found that the symptoms of high temperature-stress in plants were more severe when combined with water stress. One of the symptoms identified by De Boeck et al. (2016) was reduced nutrient uptake. Under conditions

of high temperature stess vapour pressure deficits (the difference between the actual- and saturation-vapour pressure) increase which increase plant transpiration rates (Konings et al. 2017). Under circumstances of low soil water, high vapour pressure defitcits lead to greater water loss by the plant to the atmostphere. To protect against this unsustainable water loss to the atmosphere during high temperature stress plants undergo physiological responses (such as stomatal closure and wilting) which restrict water loss (Farooq et al. 2009). However, as nutrient uptake is a function of traspiration rates, during periods of high temperature stress plant nutrient uptake may be inhibited (Barber 1995). Prolonged periods of high temperature stress can also inhibit root growth thereby restricting a plant's access to nutrients (Fahad et al. 2017). Thus high temperatures impact plant functionality by restricting plant water (and thereby nutrient) uptake.

Despite the importance of rainfall, Collins et al. (2012) argue that other factors such as soil nutrient status, fire and herbivory have stronger impacts on grassland community dynamics. Studying long term interactions between these three influencers and climatic influencers of grassland productivity in response to other stressors may provide further insight into grassland community functionality. Alterations to the processes influencing grassland plant functionality via resource competition (in the form of aboveground disturbances or belowground resource release, for example) may shift the grassland community's successional trajectory (Hooper et al. 2005; Mason et al. 2011; Isbell et al. 2013a). Furthermore, greater species diversity is a strong driver of resource competition in grasslands (Tilman 2004; Wright et al. 2014). This increased competition together with more complex species interactions is often proposed as an important mechanism maintaining grassland community stability (often measured as the inverse of the coefficient of variation of a common ecosystem function such as biomass production) (Suttle et al. 2007; Hector et al. 2010; Wilcox et al. 2017b). Maintaining grassland stability is important because of humanity's dependence on grasslands for a variety of services (Soliveres et al. 2016a; Sasaki et al. 2019). Therefore, how grassland stability responds to anthropogenic impacts (an important one being alterations to nutrient status) is currently a major research focus (e.g. Borer et al. 2014a; Hautier et al. 2014; Hautier et al. 2015; Blüthgen et al. 2016).

In-situ investigations exploring grassland community responses to climatic variations and anthropogenic impacts are uncommon. Given the importance of these interactions for grassland ecosystem productivity, this study aims to explore how the short term magnitude, variability, and stability of grassland productivity responds to climatic stress (in the form of high temperatures) following nutrient additions. We utilised data collected from a long term ecological research experiment manipulating grassland soil nutrient availability at two levels (unfertilised Control and nutrient enriched) and compared growing season aboveground productivity (as RUE) to maximum growing season temperature means and standard deviations at annual and consecutive three-year time scales. As nutrient enrichment dramatically reduced grassland plant species richness and diversity, and because biodiversity is thought to mediate resistance to stress, we predicted more stable responses from the more diverse, Control grasslands.

2.2 Methods and materials

2.2.1 Site description

Analyses were based on data collected from the Veld Fertiliser Trial (VFT) conducted at the University of KwaZulu-Natal's Ukulinga Research Farm in KwaZulu-Natal, South Africa

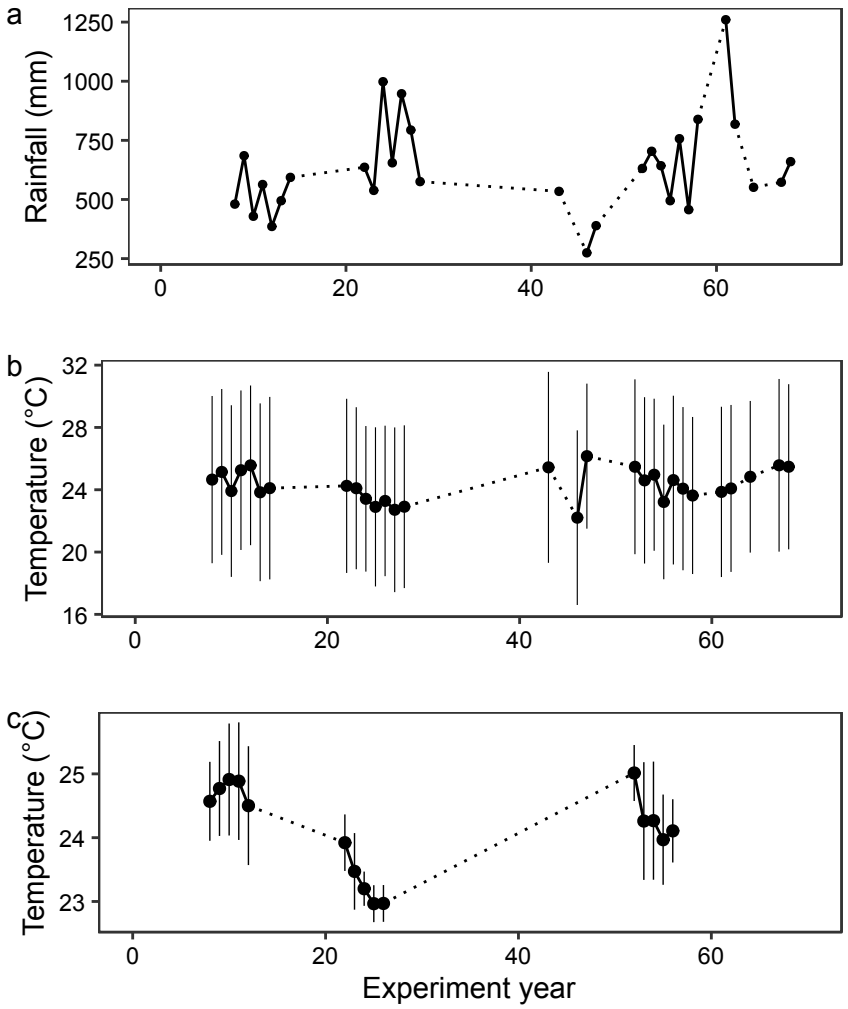

Figure 2.1: Climatic summaries for Ukulinga Research Farm (Pietermaritzburg, South Africa) from 1958 to 2009. **a** - total growing season precipitation. **b** - annual growing season mean maximum temperature ($\pm$ 1 standard deviation (SD)). **c** - consecutive three-year maximum growing season temperature ($\pm$ 1 SD). Dotted lines indicate years not included in these analyses either due to insufficient biomass or climatic data.

(29°40'11''E, 30°24'05"S). The experimental area is a perennial grassland containing numerous grass and forb species. The experimental site is located on a plateau with shallow shale-based soils. Annual and three-year rainfall and temperature metric ranges have varied over the experimental period (Figure 2.1). Furthermore, rainfall and temperature at this site are distinctly seasonal with ANPP (aboveground net primary production) being largely dependent on the current season's rainfall (Knapp et al. 2006). The growing season runs from the first spring rains in September/October until March/April.

2.2.2 Experimental design and data collection

The VFT was initiated in 1951 with the aim of understanding nutrient addition impacts on grassland productivity. The trial is arranged in a randomised block design with a total of 16 nutrient enrichment treatments although only the Control (no nutrient input; $n = 6$ plots) and the highest level of Nutrient enrichment (limestone ammonium nitrate (28 %N) applied at a rate of $21\,g.m^{-2}.yr^{-1}$; superphosphate (11.3 % P) applied at a rate of $3.8\,g.m^{-2}.yr^{-1}$; dolomitic lime applied at a rate of $225\,g.m^{-2}.yr^{-5}$; $n = 6$ plots) were used in this study. Plots measured $2.7\,m \times 9.8\,m$. To characterise the effects that the treatments have had on grassland species composition and structure, species composition data obtained using various methods were collected in 1953, 1966, 1981, 1999, 2010, and 2019. Species composition data from 1953, 1966, 1981, and 1999 were obtained using point based methods where the nearest plant was identified. Species compositions for 2010 were obtained using the dry weight rank method (Tsvuura and Kirkman 2013). In 2019, species composition was determined from the percentage of aerial cover of each species overhanging four $1 \times 1\,m$ subplots. This was estimated visually to the nearest 1 %.

Experimental plots were initially clipped triannually (December (early growing season), March (late growing season) and July (winter season)). Only biomass data collected from the growing season cuts are used in these analyses as little growth and high temperature stress occurs during the late autumn and winter periods. There was no difference in ANPP between the number of cuts recieved within nutrient addition treatments and Nutrient enriched ANPP responses were always significantly greater than Control ANPP (see statistical analyses section for a detailed description of the analysis methodology) (Figure 2.2). Thus, increased clipping frequency did not appear to confound this study. Since approximately 1995, these plots have only received an annual late growing season clips. The total annual biomass was considered for these clip events. Prior to each clipping event biomass in the pathways between plots was clipped and removed. Following this, a single strip through the breadth of each plot (measuring $2.7m \times 2.2\,m$) was cut to approximately 10 cm above the soil, gathered together and then weighed wet *in situ*. A small representative grab sample of each plot's biomass was then collected and weighed wet and weighed again after drying at 60 °C for 48 hours. Dry matter responses (calculated as $DM = WM \times \frac{GD}{GW}$ where DM is strip dry matter, WM is strip wet matter, GD is the grab sample dry matter, GW is the grab sample wet matter) were then converted to $g \cdot m^{-2}$ for each plot. When plots were clipped twice during the growing season these production data were summed after calculating dry matter to obtain total ANPP for the whole growing season.

Climatic data (obtained from a weather station installed in 1958 and located ~550 m north and ~40 m below the trial) were collected from 1959 to 2009. Over the entire growing period (between the last cut of each previous season (on the day of either the winter or March clip event, whichever was later) and the last cut of each current growing season (March)), the mean and standard deviation of the maximum temperature (T_{max}) and total annual precipitation (TAP) were calculated for each available year from the daily weather data. Annual and consecutive three-year rain use efficiencies (RUE) were then calculated as $RUE = \frac{ANPP}{TAP}$ where $ANPP$ here is the aboveground net primary production per square meter for each plot per year. To understand which component of stability is driving changes in temporal stability (defined as the ratio of the mean productivity to the standard deviation (SD) of the productivity - $S = \frac{mean}{SD}$, Lehman and Tilman 2000) we calculated mean RUE and RUE SD over each possible consecutive three-year period (i.e. 1958 - 1960; 1959 - 1961; 1960 - 1962; etc.). We chose consecutive three-year periods as SD calculations require at least three data points. Minimising the length of the consecutive time period also allowed optimal use of the

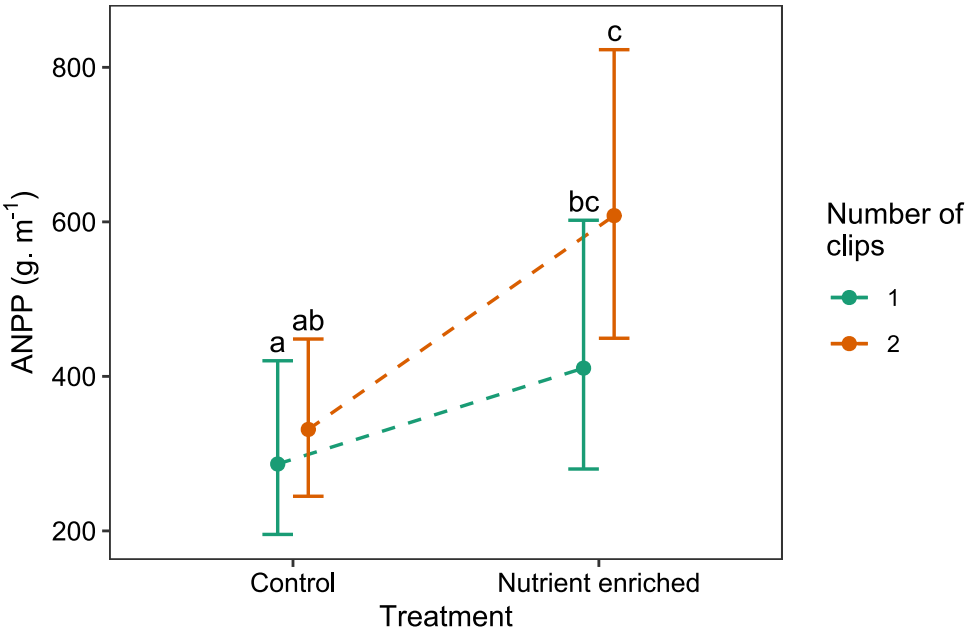

Figure 2.2: No difference in mean aboveground net primary production between the number of clips per year within nutrient addition treatments. Figure responses are back-transformed from the $\log_e$ scale. Shared letters indicate means which are not significantly different from one another.

available data given several missing observations of both biomass and climatic data which break the consecutive periods. Only years where 80% or more of the weather data were recorded were included in these analyses. Climatic data used in these analyses showed no relationships with one another on an annual scale but at three-year scales, T_{max} mean was positively correlated with T_{max} SD (Supplementary Table 2.B.2).

2.2.3 Statistical analyses

All analyses were conducted in R version 3.5.2 (R Core Team 2018). Species richness as counts and diversity as Shannon H' were calculated using the `diversity` function from the `vegan` package (Oksanen et al. 2019) for each species composition sampling year. Richness and diversity response ratios as $\frac{Nutrient\,enriched}{Control}$ of the nearest pair of Nutrient enriched and Control plots within each block were distributed by the experiment year as a continuous predictor using generalised linear models (GLM). Response ratio residuals were modelled with a gaussian error distribution and a log link function to improve residual normality. Using response ratios helped to control for the varied in species sampling methodologies used during the experiment by standardising the units. However, because of the differences in the number of species identified during the different samplings the differences between treatments within a given year may not have be controlled for effectively using this method. Within plot species heterogeneity as Bray-Curtis dissimilarity (calculated using the `vegdist` function from the `vegan` package), evenness as Simpson's Evenness calculated using the `community_structure` function from the `codyn` package (Hallett et al. 2016) and grass cover percentage of the total cover based on species cover data collected in 2019 were predicted by *Treatment* (categorical with two levels) via the `glmer` function from the `lme4` package with plot included as a random intercept to control for repeated sampling of the same plot. Residuals were modelled using binomial distributions. Logit link functions were used to ensure proportional responses.

Species rank abundances were also determined using `vegan`. These were modelled as generalised linear mixed models using a gamma error distribution and $\log_e$ link function via the `glmer` function. Rank abundance percentages were distributed by $Treatment \times Rank$. "plot" was included as a random intercept in the mixed models to Control for pseudoreplication in each of these analyses.

To assess whether there was an effect of clipping frequency on annual ANPP, Log_e transformed ANPP was modelled by Nutrient enrichment treatement by cutting frequency (both as factors) using the `lmer` function from the `lme4` package. *Season* was included as a random intercept effect. *Block* could not be included in the random effect structure as including this level resulted in singular fits. Annual RUE and three-year mean, standard deviation and stability RUE responses distributed by Nutrient enrichment treatment and temperature stress were modelled using the `lmer` function from the `lme4` package. The same model (described in (2.1)) was used for all RUE analyses except for the RUE stability response. RUE responses were $\log_e$ transformed to improve normality and to ensure positive fitted values. Diagnostic autocorrelation plots did not indicate the presence of temporal autocorrelation in the annual nor the three-year models and so an autoregressive structure was not included in these models. We used the `step` function from the `lmerTest` package (Kuznetsova et al. 2017) to determine the optimum random effect structure to account for variation across years and across spatial blocks. "year" was identified as the optimal random intercept for all models.

$$\begin{aligned} RUE_{ijk} &\sim Gaussian(\mu_{ijk}) \\ E(RUE_{ijk}) &= \mu_{ijk} \\ log_e(\mu_{ijk}) &= Treatment_{ijk} + Mean\,T_{max_{ijk}} + T_{max_{ijk}}SD + \\ &\quad Mean\,T_{max_{ijk}} \times Treatment_{ijk} + \\ &\quad T_{max_{ijk}}SD \times Treatment_{ijk} + \\ R_{ij} &\sim N(0, \sigma^2) \end{aligned} \tag{2.1}$$

where RUE_{ijk} is the k^{th} plot observation within block j nested within year i. The random effect structure is assumed to be normally distributed with mean 0 and variance σ^2. Parameter significance was determined using the `anova` function from the `stats` package for GLM, the `anova` function from the `lmerTest` package for LMM and the `Anova` function from the `car` package (Fox and Weisberg 2019) for GLMM. Pairwise comparisons of significant effects were carried out using the `emmeans` and `emtrends` functions from the `emmeans` package (Lenth 2019). Comparisons were conducted and differences are presented on the link scale. Grass cover estimates are presented as mean cover (95% confidence intervals). Significance was determined at $\alpha = 0.05$.

2.3 Results

2.3.1 Sward composition

The species richness response ratio $\left(\frac{Nutrient\,enriched}{Control}\right)$ (Figure 2.3a) revealed no differences in the number of species at the beginning of the experiment (t-value = -0.108, $p = 0.915$). This ratio decreased over time from the start of the experiment (t-value = -3.387, $p = 0.002$) indicating greater species numbers in the Control plots. Diversity as Shannon H' (Figure 2.3b)

was similar between Nutrient enriched and Control grasslands at the beginning of the experiment (t-value = -0.129, p = 0.898) with this ratio declining significantly through time

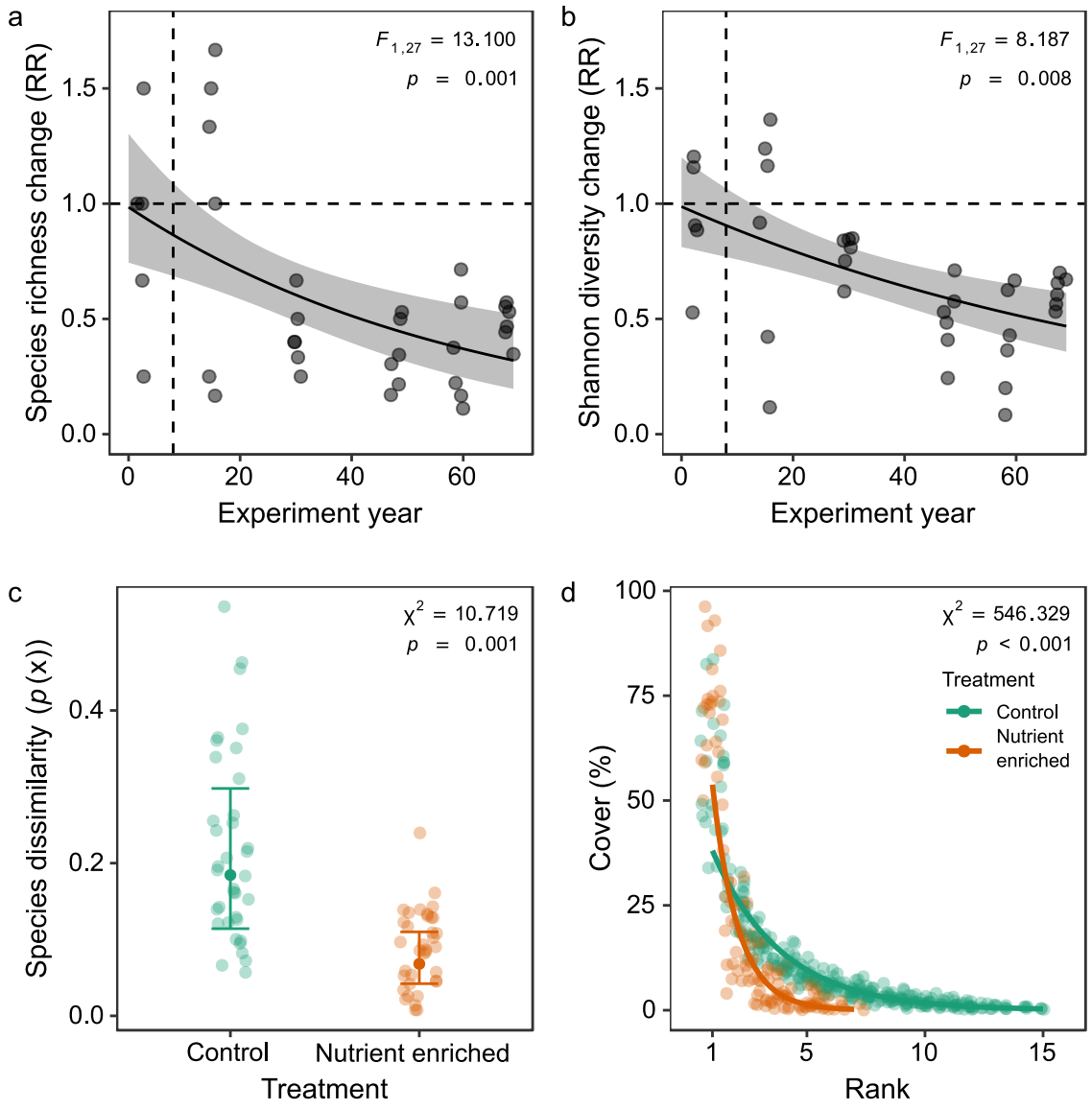

Figure 2.3: Effects of nutrient enrichment on grassland sward characteristics. Response ratios (RR, $\frac{Nutrient\ enriched}{Control}$) of species richness (**a**) and species diversities (as Shannon H', **b**) throughout the experimental period. Horizontal dotted lines indicate the line of no effect (RR = 1, responses do not differ between treatments). Values above and below this line indicate more positive and more negative richness or diversity responses following nutrient enrichment, respectively. Vertical dotted lines indicate the first year of rain use efficiency data included in the subsequent analyses. **c** - Within plot Bray-Curtis dissimilarities. **d** - Species rank abundances patterns. Figure responses are back-transformed from the link scale. Data points are jittered horizontally to show overlap. Data were collected from the Veld Fertiliser Trial initiated in 1951 at the Ukulinga Research Farm (Pietermaritzburg, South Africa). Species composition surveys took place in 1953, 1966, 1981, 1999, 2010 and 2019. Figures 2.2c and d were produced from data collected in 2019.

(t-value = -3.747, p = 0.0007). Species Bray-Curtis dissimilarity in 2019 differed between

treatments ($\chi^2_1 = 10.719$, $p = 0.0011$, Figure 2.3c) with Control grasslands showing greater within-plot dissimilarity than Nutrient enriched grasslands. Species cover abundances (Figure 2.3d) declined significantly as the rank number increased (Supplementary Table 2.B.3, $p < 0.0001$). These slopes also differed between treatments (Supplementary Table 2.B.3, $p < 0.0001$) with Nutrient enriched grasslands showing more negative slopes than Control grasslands (slope difference = 0.580 (0.532, 0.629), Z-ratio = 23.374, $p < 0.0001$). Grass cover ($\chi^2_1 = 6.101$, $p = 0.0135$) was found to be lower in Control plots (67.7% (59.0%, 75.3%)) than in Nutrient enriched plots (80.5% (73.7%, 85.8%)).

2.3.2 Annual RUE

Annual RUE (model parameters and significances presented in Supplementary Table 2.B.4) differed between Nutrient enrichment treatments (Supplementary Table 2.B.4, $p < 0.0001$) with Control grasslands having lower RUE (Control mean = 0.494 (0.388, 0.628), Nutrient enriched mean = 0.812 (0.639, 1.032), mean difference = -0.498 (-0.564, -0.431), t-ratio = -14.740, $p < 0.0001$). Neither increasing mean T_{max} (Supplementary Table 2.B.4, $p = 0.291$) nor increasing T_{max} SD (Supplementary Table 2.B.4, $p = 0.690$) affected RUE. However, considering treatment responses, Control annual RUE responded less negatively to increasing mean T_{max} than did Nutrient enriched annual RUE (slope difference = 0.136 (0.063, 0.210), t-ratio = 3.635, $p = 0.0003$; Figure 2.4; Supplementary Table 2.B.4, $p = 0.0003$). No differences in responses between treatments were detected as T_{max} SD increased (Supplementary Table 2.B.4, $p = 0.653$).

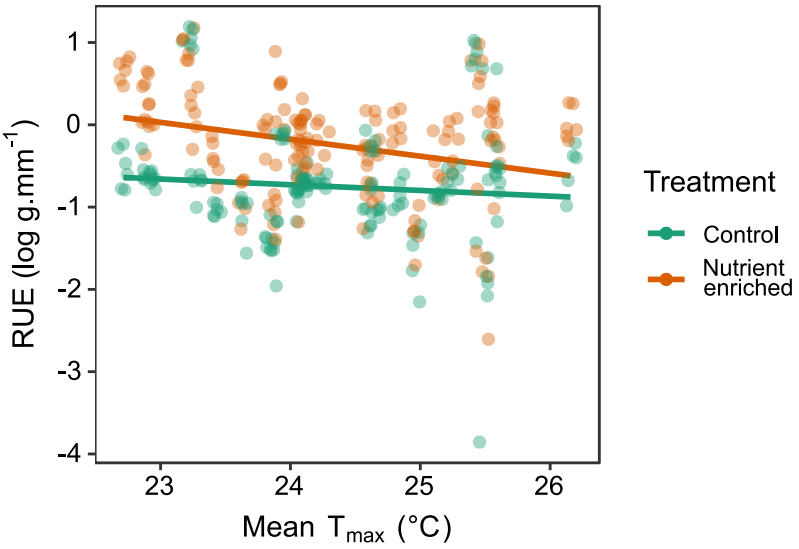

Figure 2.4: Annual rain use efficiencies (RUE) for Control and Nutrient enriched grasslands across annual mean maximum temperature. Regression responses are presented on the log e scale. Points are jittered to show overlap. Data were collected from the Veld Fertiliser Trial initiated in 1951 at the Ukulinga Research Farm (Pietermaritzburg, South Africa). Only data from 1959 until 2018 are presented.

2.3.3 Three-year RUE

Nutrient enrichment alone did not significantly affect three-year mean RUEs (Supplementary Table 2.B.5, $p = 0.081$). Mean RUE was negatively correlated with T_{max} across treatments

(Supplementary Table 2.B.5, $p = 0.003$) whilst mean RUE across treatments was positively correlated with T_{max} SD (Supplementary Table 2.B.5, $p < 0.001$). Nutrient enrichment mean RUE was less positively affected as T_{max} SD increased (Supplementary Table 2.B.5, $p = 0.007$) but not as mean T_{max} increased (Supplementary Table 2.B.5, p 0.227). Increased T_{max} SD promoted mean RUE for Control grasslands more than Nutrient enriched grasslands (slope difference = 0.540 (0.152, 0.928), t-ratio = 2.748, $p = 0.007$; Figure 2.5a).

RUE SD was not affected by Nutrient enrichment (Supplementary Table 2.B.6, $p = 0.141$) and it did not vary across increasing mean T_{max} (Supplementary Table 2.B.6, $p = 0.197$) but was positively correlated with increasing T_{max} SD (Supplementary Table 2.B.6, $p = 0.021$). Between nutrient enrichment treatments, increased mean T_{max} also did not affect RUE SD (Supplementary Table 2.B.6, $p = 0.331$) but increasing T_{max} SD caused a greater RUE SD increase for Control grasslands (slope difference = -0.406 (-0.555, -0.257), t-ratio = -5.392, $p <$ 0.0001; Figure 2.5b; Supplementary Table 2.B.6, $p < 0.0001$).

Because mean T_{max} played a relatively minor role in grassland mean RUE and RUE SD through time, its effects were excluded from the stability model. Stability regression intercepts differed between treatments (Supplementary Table 2.B.7, $p < 0.0001$) with lower stability for Nutrient enriched plots at lower temperature variability. T_{max} SD (Supplementary Table 2.B.7, $p = 0.068$) did not influence grassland RUE stability responses. However, across increasing T_{max} SD Control grassland RUE stability declined more quickly than did Nutrient enriched grassland RUE stability (slope difference = -1.302 (-1.770, -0.834), t-ratio = -5.493, p < 0.0001; Figure 2.5c; Supplementary Table 2.B.7, $p < 0.0001$).

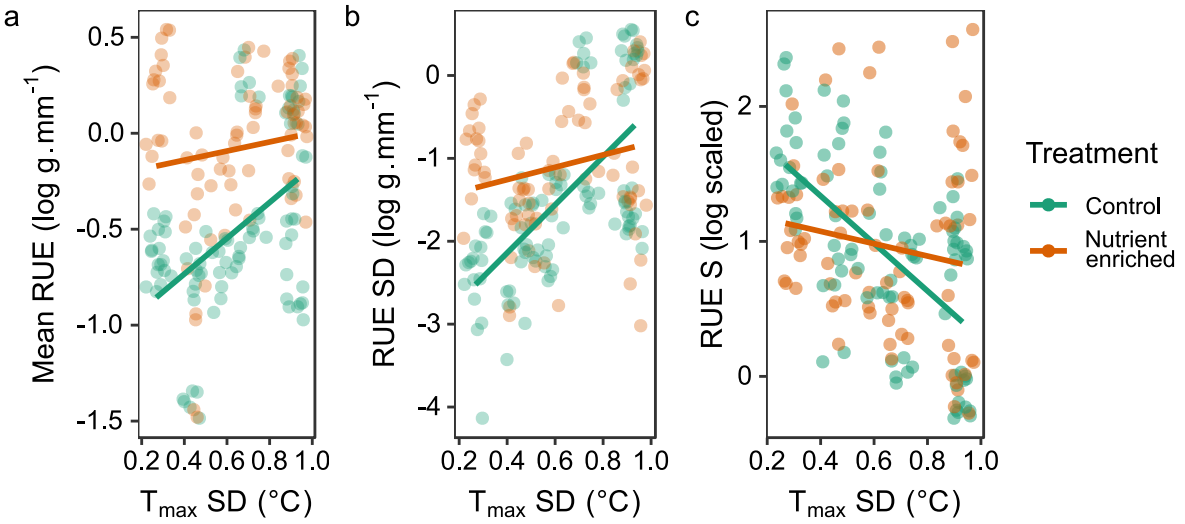

Figure 2.5: Three-year rain use efficiency (RUE) **a** - mean, **b** - standard deviation, and **c** - stability responses for Control and Nutrient enriched grasslands across increasing three-year maximum temperature standard deviations. Regressions are presented on the log$e$ scale. Points are jittered to show overlap. Data were collected from the Veld Fertiliser Trial initiated in 1951 at the Ukulinga Research Farm (Pietermaritzburg, South Africa). Only data from 1959 until 2007 are presented.

2.4 Discussion

This study explored how short-term grassland mean RUE and RUE SD changes impacted grassland RUE stability in response to high temperature stress. We found that at an annual scale despite overall lower RUE, Control grasslands maintained constant RUE across increasing mean maximum temperature. Conversely, Nutrient enriched grassland annual RUE declined as mean maximum temperature increased. Maximum temperature SD was unimportant at the annual scale. At three-year scales, maximum temperature SD was generally a better predictor of grassland stability and its constituents with Control grasslands increasing in mean RUE and RUE SD more so than Nutrient enriched grasslands. Control grassland RUE SD increased and overtook the Nutrient enriched grassland RUE SD at high maximum temperature SD. This reduced the three-year RUE stability for Control grasslands more than for Nutrient enriched grasslands.

Our findings appear to contrast with empirical theory which argues that diversity begets stability in response to disturbances (Tilman and Downing 1994). Several recent experiments have documented more diverse communities becoming less stable during disturbances, possibly due to increased species turnover rates or increased productivity (and thereby variability) as resource availability increases (Grman et al. 2010; Vogel et al. 2012; Wright et al. 2015). In our study, we found evidence of substantially reduced species diversity and biotic homogenisation following long term nutrient enrichment which is indicative of uncompetitive species being excluded from these Nutrient enriched communities. Species and functional diversity losses often cause losses of rare functional traits within the community (Suding et al. 2005). Despite their relatively small contributions to biomass, rare species presence can support ecosystem multifunctionality as they tend to have fewer function supply trade-offs than do common species possibly because they supply a wider range of functions (Soliveres et al. 2016b). Given the higher species diversity and more even rank abundance distributions observed in the Control grasslands, it is likely that these grasslands also had higher functional trait diversity than the Nutrient enriched grasslands. Why then were the Control grasslands less stable during greater climatic variability?

Annually, Control grassland RUE was unaffected by increased mean temperature stress whilst RUE in Nutrient enriched grassland was reduced to Control grassland levels during years with high maximum temperatures suggesting poorer resource use efficiencies in Nutrient enriched grasslands. During high temperature stress physiological mechanisms (e.g. transpiration and belowground to aboveground nutrient translocation rates, reduced photosynthetic ability, Alam 1999; Hu and Schmidhalter 2005; Luo et al. 2018) restrict soil nutrient availabilities. This may change across rainfall gradients with higher precipitation tending to promote nitrogen limitation which allows nutrient enriched grasslands to outperform Control grasslands during wetter years (Ren et al. 2017). This may be important for our annual RUE responses. The reduced benefit of nutrient enrichment at constant and high maximum temperatures suggests a shift in RUE limitation away from nutrients, potentially towards water limitation. Drought conditions combined with eutrophication can lead to dramatically altered soil organism structure and functioning, particularly with regards to invertebrate feeding activity. This Siebert et al. (2019) suggested reduces nutrient cycling rates. On the other hand, high temperature-stressed plants which are also well-watered experience minimal negative effects and so water (and perhaps also phosphorus, Geng et al. 2017, although unlikely in our study because of P addition) is possibly a strong controller of belowground resource availability in hot years.

Reduced three-year mean RUE occurred for both Nutrient enriched and Control grasslands as

three-year mean T_{max} increased. However, particularly for Control grasslands, mean RUE and RUE SD increased in response to maximum temperature SD. Minimising stress over several years can promote the persistence of less common species and functional groups (Knapp et al. 2001). Periods of high T_{max} SD likely have both hot and cool periods which could explain why Control grassland productivity was maximised during periods of greater T_{max} SD. However, under sustained multi-year stress (lower maximum temperature SD in our study) dominant species decline in abundance and are replaced by other species, potentially to the detriment of the whole community (Evans et al. 2011). This occurred for both our Control and, to a lesser extent, Nutrient enriched grasslands where maximum temperature variability promoted mean RUE. Less negative responses by Nutrient enriched grasslands to low maximum temperature variability suggests the persistence and increased performance of dominant species. Yet, more positive Control RUE SD responses does not imply dominant species persistence. Rather it could be an artefact of greater species turnover during variable stress as the plant community adjusts to the type of stress being applied (He et al. 2013; Cowles et al. 2016).

The stability results hint at species or functional turnover in Control grasslands during periods of variable maximum temperature stress. Although both Nutrient enriched and Control grasslands showed increased mean RUE under climatic variability, Control grassland RUE SD increased more dramatically than its mean RUE. Control grassland RUE stability reductions during variable maximum temperature periods were, therefore, due to increased RUE variability rather than reduced mean RUE. This situation is suggestive of a change in the community's state as these communities often experience instability during species turnover periods (Stampfli and Zeiter 2004; Grime et al. 2008; Cowles et al. 2016; Jones et al. 2017). In a synthesis of the available species turnover studies Anderson (2007) showed that turnover rates are highest at the beginning of the successional process but then these rates decline exponentially through time. The increased RUE SD of the more diverse Control grasslands could be indicative of a regression in successional state. Alternatively, it could be that some of the many species present in these Control grasslands persisted through the disturbance (perhaps because of underground storage organs which are common in natural grasslands, Fynn et al. 2005; Zaloumis and Bond 2011) but were for a time dormant or unproductive.

Little change in Nutrient enriched grassland stability is likely due to the persistence of species which are resilient to high temperature stress. Grman et al. (2010) reported that more stable, low diversity grasslands were dominated by highly abundant species. Dominant species identity is important for understanding community assembly (Avolio et al. 2019), however, differences in both rank abundance distributions and diversity indices revealed differences in both structure and composition between the Nutrient enriched and Control grasslands used in our study. Both Control and Nutrient enriched grasslands showed almost equal species evenness which contrasts the rank abundance responses but this is likely due to the co-linear relationship that commonly occurs between community species richness and evenness (Smith and Wilson 1996). In a temperature stress context, Olsen et al. (2016) hypothesised that inter-plant dynamics may shift from facilitation towards competition with the more competitive species eventually dominating the stressed communities. Species which can successfully persist and compete in temperature stressed grasslands are usually grasses owing to their greater water use efficiency than forbs and sedges (Fridley et al. 2016) and their deeper rooting depth and greater leaf dry matter content (Polley et al. 2013). Carlsson et al. (2017) confirmed this by showing that *in situ* grassland resilience to drought is dependent on a high proportion of grasses within the community. Graminoid persistence in our Nutrient enriched grasslands historically (Tsvuura and Kirkman 2013; Ward et al. 2017) and currently in 2019 suggests that these communities are well adapted to temperature stress.

Despite the seemingly positive results from the Nutrient enriched plots in this study, we caution that their apparent resilience to climatic stress may be superficial. Species losses following nutrient enrichment are likely to persist for many decades (Isbell et al. 2019). During this time these low diversity grasslands may be exposed to various combinations of stressors. When press (warming, nitrogen deposition, altered rainfall patterns) and pulse (fire) disturbances co-occur more dramatic shifts in community composition are more likely (Collins et al. 2017), possibly because of a functional trait deficit within the community. Given the high occurrence of pulse disturbances in mesic sub-Saharan grasslands (Midgley and Bond 2015), we hypothesise that Nutrient enriched grasslands will deteriorate more quickly than Control grasslands when exposed to natural disturbances or changes in management regime in combination with climatic stress. We suggest this because although Nutrient enriched grasslands can be stable despite consisting of only a few, highly dominant species, reduced diversity resulting from nutrient deposition causes species synchrony – an hypothesised driver of community stability (Hautier et al. 2014; Blüthgen et al. 2016; Wilcox et al. 2017a). More simply, if disturbances can eliminate dominant species from nutrient enriched grassland communities, the community will likely collapse as there are few other species present in the community to offset the loss of these dominant species.

Resistance to climatic disturbance is also not the only important consideration for grassland ecosystem stability. Recovery from disturbance also plays a key role and may be strongly related to plant reproductive mechanisms such as seed germination (Stampfli and Zeiter 2004). Production and diversity in nutrient enriched communities are often limited by light availability with low light availability negatively impacting seedling establishment (and perhaps seed production through tillering) (Hautier et al. 2009). In some cases, nutrient enriched grasslands may take several decades for species diversity to be restored passively (Isbell et al. 2013a; Isbell et al. 2019). Thus, despite displaying greater resistance to climatic stress, nutrient enriched grasslands may struggle to recover compositionally following combinations of stressors. Our observations of lower stability in Control grasslands are in line with the description of variable communities in disturbance mediated grasslands by Midgley and Bond (2015). This raises concerns of how the ecosystem stability concept should be applied in disturbance mediated grasslands, especially given the close link of biodiversity, ecosystem stability and ecosystem services (Hooper et al. 2005). As our global climate becomes increasingly unpredictable land managers can no longer manage their lands with the aim of maintaining or increasing grassland productivity. Perhaps what is needed is increased focus towards managing grasslands for resillience to (multiple) stressors especially given the important impacts that global change is having on important human activities (e.g. agricultural productivity Thornton et al. 2014; Ray et al. 2015). Perhaps the problems that the agricultural sector is facing (such as increased yield variability and greater disease and pest outbreaks) could be addressed through increased diversification within the agricultural sector. Further research and discussions are needed to understand how ecosystem functioning can be maintained in intrinsically dynamic species compositions.

By using RUE as a measure of absolute community productivity, our work suggests that greater biodiversity does not always improve stability in response to environmental stress. To account for this we suggest that greater Control grassland variability may be a sign of a community dynamically responding, perhaps positively, to variable environmental conditions. Grassland management will benefit from further work investigating the *in situ* temporal dynamics of natural versus anthropogenically modified grasslands in response to climatic variability. This will improve our understanding of grassland state transitions exposed to global change drivers (perhaps from species identity, species dominance, or functional trait

perspectives, e.g. Hallett et al. 2014; Avolio et al. 2019) to improve ecosystem resilience in the face of global change.

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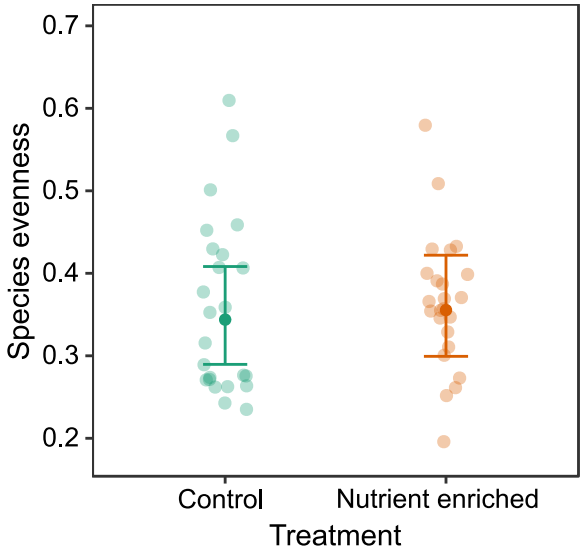
Supplementary materials

2.A Supplementary figure



Supplementary Figure 2.A.1: No difference in Simpson's Evenness between Control and Nutrient enriched grasslands. Responses are presented on the response scale where 0 indicates a plant community dominanted by a single species and 1 indicates a plant community where many species have similar abundances. Points are jittered horizontally to show overlap. Data were collected from the Veld Fertiliser Trial initiated in 1951 at the Ukulinga Research Farm (Pietermaritzburg, South Africa). Species composition surveys took place in 2019.

2.B Supplementary tables

Supplementary Table 2.B.1: A simple longtable example

Year	Species composition method	Number of mows	Biomass data	Rainfall data	Temperature data
1950		3	Yes	0	0
1951		3	Yes	0	0
1952		3	Yes	0	0
1953	Nearest plant	3	Yes	0	0
1954		3	Yes	0	0
1955		3	Yes	0	0
1956		3	Yes	0	0
1957		3	Yes	0	0
1958		3	Yes	0	0
1959		3	Yes	365	365
1960		3	Yes	365	362
1961		3	Yes	365	365
1962		3	Yes	365	358
1963		3	Yes	365	359

Continued on next page

Table 2.B.1 – *Continued from previous page*

Year	Species composition method	Number of mows	Biomass data	Rainfall data	Temperature data
1964		3	Yes	365	365
1965		3	Yes	365	357
1966	Nearest plant	3	Yes	273	268
1967		3	Yes	0	0
1968		3	Yes	0	0
1969		3	Yes	0	0
1970		3	Yes	0	0
1971		3	Yes	0	0
1972		3	Yes	0	0
1973		3	Yes	122	117
1974		3	Yes	365	365
1975		3	Yes	365	354
1976		3	Yes	365	362
1977		3	Yes	365	365
1978		3	Yes	365	365
1979		3	Yes	365	365
1980		3	No	366	366
1981	Nearest plant	3	No	365	365
1982		3	No	365	365
1983		3	No	365	363
1984		3	No	365	366
1985		3	No	365	365
1986		3	No	365	364
1987		3	No	365	365
1988		3	No	365	366
1989		3	No	365	361
1990		3	No	365	365
1991		3	No	365	365
1992		3	No	365	365
1993		3	No	365	332
1994		3	Yes	365	365
1995		1	No	220	214
1996		1	Yes	339	325
1997		1	Yes	277	313
1998		1	Yes	354	355
1999	Nearest plant	1	Yes	119	119
2000		1	Yes	293	356
2001		1	No	87	100
2002		1	Yes	57	57
2003		1	Yes	365	168
2004		1	Yes	366	327
2005		1	Yes	339	314
2006		1	Yes	300	300
2007		1	Yes	365	364
2008		1	Yes	366	366

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Table 2.B.1 – *Continued from previous page*

Year	Species composition method	Number of mows	Biomass data	Rainfall data	Temperature data
2009		1	Yes	322	365
2010	Dry weight rank	1	No	365	365
2011		1	Yes	365	364
2012		1	Yes	366	366
2013		1	No	365	365
2014		1	Yes	365	365
2015		1	Yes	365	365
2016		1	No	366	366
2017		1	Yes	365	365
2018		1	No	365	365
2019	Aerial cover	1	No	135	135

Supplementary Table 2.B.2: Linear regression slope results describing the relationships between climatic variables measured at the Ukulinga Research Farm (Pietermaritzburg, South Africa) which were used in subsequent analyses

Time scale	Predictor	Response	Slope estimate	SE	t-value	p-value
Annual	Rainfall	T_{max} Mean	0.000	0.000	-1.026	0.314
Annual	Rainfall	T_{max} SD	0.000	0.000	-0.861	0.397
Annual	T_{max} Mean	T_{max} SD	0.003	0.012	0.218	0.829
Three-year	T_{max} Mean	T_{max} SD	0.478	0.123	3.896	0.0018

Supplementary Table 2.B.3: Statistical model for the effects of nutrient enrichment on plant species rank-abundance relationships

	Value	SE	t-value	p-value
(Intercept)	3.639	0.223	16.301	<0.0001
rank	-0.344	0.007	-50.561	<0.0001
treatmentNutrient	0.346	0.305	1.132	0.2574
rank:treatmentNutrient	-0.580	0.025	-23.374	<0.0001

Generalised linear mixed-effects model of species cover responses was fit by maximum likelihood. A gamma error distribution was used to model the residuals and a log link function was used to ensure positive model fits. Plot (SD = 0.252) was included as a random intercept for this model. The intercept is the estimated abundance of the most abundant species (rank = 1) in the Control plots. Data were collected from the Veld Fertiliser Trial initiated in 1951 at the Ukulinga Research Farm (Pietermaritzburg, South Africa). Species composition surveys took place in 2019.

Supplementary Table 2.B.4: Statistical model for the effects of nutrient enrichment, annual mean maximum temperature, the standard deviation of annual maximum temperature and the interactions of these two temperature metrics with nutrient enrichment on annual rain use efficiency

	Value	SE	DF	t-value	p-value
(Intercept)	0.135	3.400	25.043	0.040	0.9687
treatmentNutrient	4.051	0.984	293.002	4.118	<0.0001
tmax.sd	0.159	0.343	25.094	0.464	0.6464
tmax.mean	-0.069	0.129	25.105	-0.537	0.5959
treatmentNutrient:tmax.mean	-0.136	0.038	293.013	-3.635	3e-04
treatmentNutrient:tmax.sd	-0.045	0.100	293.011	-0.450	0.6532

Linear mixed-effects model of log transformed temporal mean RUE responses was fit by restricted maximum likelihood. t-tests were conducted using the Satterwaite method. Season (SD = 0.593) was included as a random intercept for this model. The intercept is the estimated mean value of the Control plots where mean T_{max} and T_{max} SD = 0. Data were collected from the Veld Fertiliser Trial initiated in 1951 at the Ukulinga Research Farm (Pietermaritzburg, South Africa).

Supplementary Table 2.B.5: Statistical model for the effects of nutrient enrichment, consecutive three-year mean maximum temperature, the standard deviation of consecutive three-year maximum temperature and the interactions of these two temperature metrics with nutrient enrichment on consecutive three-year mean rain use efficiency

	Value	SE	DF	t-value	p-value
(Intercept)	9.957	3.067	13.517	3.247	0.0061
treatmentNutrient	2.850	1.624	147.000	1.755	0.0813
tmax.sd	1.826	0.371	13.517	4.921	2e-04
tmax.mean	-0.482	0.134	13.517	-3.605	0.003
treatmentNutrient:tmax.mean	-0.086	0.071	147.000	-1.214	0.2265
treatmentNutrient:tmax.sd	-0.540	0.196	147.000	-2.748	0.0067

Linear mixed-effects model of log transformed temporal mean RUE responses was fit by restricted maximum likelihood. t-tests were conducted using the Satterwaite method. Season (SD = 0.237) was included as a random intercept for this model. The intercept is the estimated mean value of the Control plots where mean T_{max} and T_{max} = 0. Data were collected from the Veld Fertiliser Trial initiated in 1951 at the Ukulinga Research Farm (Pietermaritzburg, South Africa).

Supplementary Table 2.B.6: Statistical model for the effects of nutrient enrichment, consecutive three-year mean maximum temperature, the standard deviation of consecutive three-year maximum temperature and the interactions of these two temperature metrics with nutrient enrichment on consecutive three-year rain use efficiency standard deviation

	Value	SE	DF	*t*-value	*p*-value
(Intercept)	6.533	8.568	12.9	0.762	0.4595
treatmentNutrient	5.220	3.525	147.0	1.481	0.1408
tmax.sd	3.664	1.037	12.9	3.535	0.0037
tmax.mean	-0.427	0.373	12.9	-1.143	0.2739
treatmentNutrient:tmax.mean	-0.150	0.154	147.0	-0.975	0.3311
treatmentNutrient:tmax.sd	-1.904	0.427	147.0	-4.465	<0.0001

Linear mixed-effects model of log transformed temporal mean RUE responses was fit by restricted maximum likelihood. *t*-tests were conducted using the Satterwaite method. Season (SD = 0.654) was included as a random intercept for this model. The intercept is the estimated mean value of the Control plots where mean T_{max} and T_{max} SD = 0. Data were collected from the Veld Fertiliser Trial initiated in 1951 at the Ukulinga Research Farm (Pietermaritzburg, South Africa).

Supplementary Table 2.B.7: Statistical model for the effects of nutrient enrichment, consecutive three-year mean maximum temperature, the standard deviation of consecutive three-year maximum temperature and the interactions of these two temperature metrics with nutrient enrichment on consecutive three-year rain use efficiency stability

	Value	SE	DF	*t*-value	*p*-value
(Intercept)	2.040	0.384	14	5.309	1e-04
treatmentNutrient	-0.783	0.160	146	-4.884	<0.0001
tmax.sd	-1.759	0.568	14	-3.097	0.0079
treatmentNutrient:tmax.sd	1.302	0.237	146	5.493	<0.0001

Linear mixed-effects model of log transformed temporal mean RUE responses was fit by restricted maximum likelihood. *t*-tests were conducted using the Satterwaite method. Season (SD = 0.473) was included as a random intercept for this model. The intercept is the estimated mean value of the Control plots where mean T_{max} and T_{max} SD = 0. Data were collected from the Veld Fertiliser Trial initiated in 1951 at the Ukulinga Research Farm (Pietermaritzburg, South Africa).

Chapter 3

Environmental controllers of grassland stability responses to nutrient addition

Abstract

Globally grasslands are being impacted by human activities which are affecting the ability of grasslands to provide ecosystem services and functions. An important driver of global change in grasslands is increased nitrogen deposition which disrupts belowground competition, eliminates uncompetitive species and reduces the stabilising effect of species diversity. Whilst there is a substantial body of evidence showing how grassland stability changes in response to anthropogenic activities and changes in diversity, whether there are particular environmental conditions which predispose grassland communities to become unstable remains poorly understood. We explored how grassland stability over consecutive three-year periods responds to nutrient addition in a globally replicated grassland nutrient addition experiment. Sixty-two different sites across five continents with variable climatic, management, edaphic and sward structural conditions were considered in this investigation. We found that African and North American grassland stability responded negatively to nutrient addition. Nutrient addition increased stability in artificially created grasslands but reduced stability in grasslands with a burning regime. Changes in both soil nutrient availability and soil nutrient contents (of macronutrients but not micronutrients) induced by nutrient addition also drove changes in stability. Regions where nutrient addition reduced species asynchrony, increased compositional dissimilarity or increased species evenness were also associated with reduced stability. These results will be useful for informing policy and management decisions and guidelines concerning human activities in grasslands.

Keywords: *Anthropogenic global change* • *Eutrophication* • *Grassland ecosystem functioning* • *Nutrient Network Experiment* • *Sward structure*

3.1 Introduction

Monitoring ecosystem stability can provide insight into plant community responses to surrounding factors (both anthropogenic and environmental) which may impact ecosystem sustainability. Early hypotheses to explain ecosystem stability proposed that more diverse plant communities would likely show less dramatic functional variation in response to

environmental change (McNaughton 1977). Tilman and Downing (1994) provided evidence in support of this hypothesis by showing that the productivity of grasslands with more species respond less negatively to drought than grasslands with fewer species. The mechanisms behind these responses have been intensely debated over the past decades (Grimm and Wissel 1997; Ives et al. 2000; McCann 2000; Ives and Carpenter 2007). Recent developments have put forth both experimental and observational support for the hypothesis that asynchronous species fluctuations through time in response to environmental fluctuations are believed to maintain community stability (Loreau and de Mazancourt 2008; Hector et al. 2010; Hautier et al. 2014; Blüthgen et al. 2016; Wilcox et al. 2017b). However, in some cases species dominance rather than diversity may promote stability more stability under certain circumstances (Grman et al. 2010; Yang et al. 2018).

Although ecosystem stability can be measured across space (Fuhlendorf and Engle 2004; Hovick et al. 2015), when measured across time the focal community is a single area experiencing environmental change rather than a larger area characterised by heterogeneous environmental conditions. Large, heterogeneous areas are becoming increasingly uncommon as anthropogenic impacts transform variable landscapes into biotically and environmentally homogenous units (Gossner et al. 2016). These transitions eventually reduce the simultaneous supply of multiple functions from ecosystems (Hector and Bagchi 2007; Lefcheck et al. 2015; Hautier et al. 2018).

In naturally assembled ecosystems stability is dependent on species interactions. These interactions can take the form of competition for shared resources with more competitive species generally being able to persist through perturbations (Tilman et al. 1998). Alternatively, species which are capable of using a wider range of resources or which can withstand periods of nutrient deficiency could give these species an advantage over those which are only capable of persisting when all resources are available to them. They do this by diversifying the risk and protecting against yield instability thereby increasing their probability of persisting through disturbances (Loreau and de Mazancourt 2008; de Mazancourt et al. 2013) or changes in ecosystem state (for example through invasion; Zavaleta 2004; Selmants et al. 2012). Biodiversity appears to have a general stabilising effect on plant communities across the globe with how the various species within a plant community respond to environmental fluctuations often being proposed as the link between diversity and stability (Hautier et al. 2014; Wilcox et al. 2017a; Craven et al. 2018). However, the environmental factors influencing stability remain less well understood (Donohue et al. 2016; van der Plas 2019). Given the strong link between plant species' phenologies and the environmental conditions through which plant species can persist (Butler et al. 2017; Bruelheide et al. 2018), there may be strong environmental influences or predictors of community stability.

Human activities can also affect ecosystem stability (MacDougall et al. 2013; Hautier et al. 2015; Blüthgen et al. 2016). Given the wide-reaching nature of anthropogenic change and the associated impacts on plant community structure and functioning (Vitousek 1994; Ellis et al. 2010; Murphy and Romanuk 2014; Midgley and Bond 2015), it is important to understand which non-anthropogenically controlled environmental conditions could predispose plant communities to periods of instability. Globally, plant species diversity varies across environmental conditions. For example, plant species richness and its response to human activities can vary spatially (Stevens 2004; Gillman et al. 2015). Climatic variation may influence the importance of biodiversity in promoting community stability (Hallett et al. 2014; García-Palacios et al. 2018) and changes in soil physical and biotic components can also translate into plant community instability (Yang et al. 2018). Some studies have explored

stability in response to environmental gradients at large, sometimes continental, scales (Ivits et al. 2016), however, few comprehensive global assessments of stability exist. Those that do (e.g. Hautier et al. 2014; Wilcox et al. 2017a; Craven et al. 2018) did not directly consider the broad ranges of environmental factors which could predispose to dramatic changes in ecosystem function sustainability.

To accurately inform policy decisions relating to ecosystem management, it is important to understand how anthropogenic activities impact different kinds of ecosystems and which ecosystems are more sensitive to anthropogenic activities. This study therefore aims to understand how grasslands with different environmental conditions respond to human activity in the form of nutrient addition. Here, we use a globally replicated grassland experiment to explore changes in ecosystem stability following nutrient addition across several environmental gradients. Specifically, we consider latitude and elevation, precipitation and potential evapotranspiration, management history, changes in soil properties and changes in grass sward characteristics following eutrophication.

3.2 Materials and methods

3.2.1 Site description

The Nutrient Network experiment is a global grassland experiment manipulating belowground resources through nutrient addition at various levels, and aboveground defoliation via herbivore exclusion at research sites across the globe (Borer et al. 2014a). The experimental design used in this study's analyses is a randomised block design of plots ($5 \times 5\ m^2$) within blocks (range = 1:6, mean = 3.15 ± 0.88 SD) within sites ($n \leq 62$; Figure 3.1). For some analyses, fewer sites were used because of missing data.

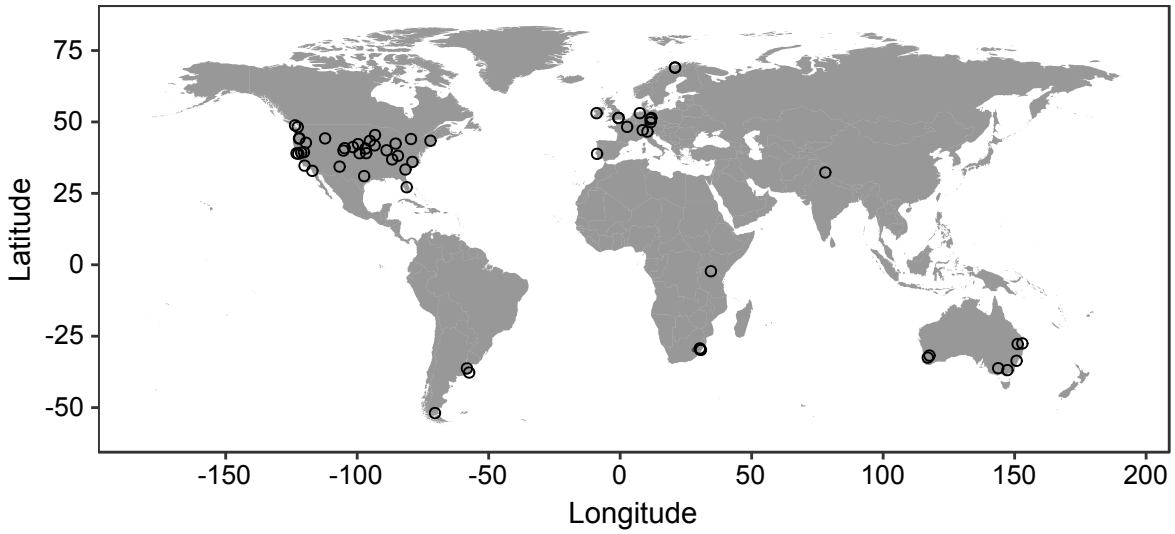

Figure 3.1: Global distribution of sites ($n = 62$) used in these analyses (open circles).

3.2.2 Experimental treatments

Plots were selected from Nutrient Network sites which applied full factorial combinations of nutrient additions in the form of nitrogen (N), phosphorus (P) and potassium application with a micronutrient mix ($K_{+\mu}$) for at least three years. For sites which have been running for more

than eight years, only data from the first eight years were used. Within blocks, plots were separated from one another by a walkway (1 m) and a buffer zone (0.5 m along the edge of each plot). This controlled for the impacts that treatments applied to neighbouring plots may have had on one another. N, P and K are applied annually with 10 $g\ N \cdot m^{-2} \cdot year^{-1}$ as time-released urea $[(NH_2)_2CO]$, triple-super phosphate $[Ca(H_2PO_4)_2]$ at 10 $g\ P\ m^{-2}\ yr^{-1}$ and 8.1 $g\ Ca\ m^{-2}\ yr^{-1}$, and potassium sulphate $[K_2SO_4]$ at 10 $g\ K\ m^{-2}\ y^{-1}$ and 3.9 $g\ S\ m^{-2}\ yr^{-1}$, respectively. At the start of the experiment a single 100 $g \cdot m^{-2}$ micronutrient mix of Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), Cu (1%), Zn (1%), B (0.2%) and Mo (0.05%) was added to the plots receiving the potassium treatment. Factorial treatment combinations (8 combinations) were applied within each block. Treatment applications were applied consistently across sites.

3.2.3 Environmental variables

Site level descriptors

Site-level descriptors were collected from local investigators. These included site coordinates, continent and elevation, the management practices and history at the site (burned, grazed, mowing, and whether the site was natural or anthropogenically created through restoration or cultivation (coded as "Anthropogenic")). Where available, climatic data were sourced and supplied by local investigators from a weather station near to each site.

Soil properties

Before experimental treatments were applied and after three years of treatment application, two 2.5 cm soil cores were collected from each plot. Samples from each plot were combined into a single homogenous sample and dried. Soil N from each plot was analysed in a single analytical laboratory using a Costech ECS 4010 CHNSO Analyzer on pulverised soil (Knops Lab, University of Nebraska, USA). Extractable soil P, K, micronutrients, pH, cation exchange capacity (CEC) and organic matter content (OM) for every soil sample also were quantified in a single analytical laboratory using standard methods (A & L Laboratories, Memphis, Tennessee, USA).

Species diversity

Within each 5×5 m plot, a randomly selected, permanent 1×1 m subplot was identified and the percentage aerial cover of each species overhanging the subplot was estimated visually to the nearest 1 % annually. Where present bare ground, litter, rock, soil, and woody plant cover were included in these assessments but were not included as pseudo-species in these analyses. These cover data were used to calculate Simpson's diversity (using (3.1) where p_i is the proportional abundance of species i in a plot with S species) and Piloue's species evenness (using (3.2) where p_i is the proportional abundance of species i in a plot with S species) for the pre-treatment year and the third post-treatment year. We calculated Bray-Curtis dissimilarity between the pre-treatment year and the third post-treatment year. We also calculated species asynchrony (using (3.3) where σ^2 is the temporal standard deviation in abundance of species i in a plot with S species across the first three years following treatment application) following Loreau and de Mazancourt (2008). Species abundances calculated as the relative percentage cover multiplied by the net aboveground primary productivity were used instead of percentage cover for species asynchrony calculations (as in Hautier et al. 2014).

$$D = 1 - \sum_{i=1}^{S} p_i^2 \tag{3.1}$$

$$J = \frac{-\sum_{i=1}^{S} p_i log_e p_i}{log_e S} \tag{3.2}$$

$$1 - \varphi_b = 1 - \frac{\sigma^2}{\left(\sum_{i=1}^{s} \sigma_i\right)^2} \tag{3.3}$$

Total plant biomass

Adjacent to the permanent 1×1 m cover subplot, all rooted plant biomass was harvested from two 1×0.1 m strips by clipping at ground level. Biomass samples were then dried at 60 °C for 48 hr. Samples were weighed to the nearest 0.001 g and multiplied by five to obtain an estimate of grams per square meter. Biomass samples were collected towards the end of the growing season.

Ground level light availability

Light availability (as photosynthetically active radiation; PAR, μmol photons per m^2 per s) was obtained using a 1-m light ceptometer. One above canopy and two ground level measurements were taken annually towards the end of the growing season between 11h00 and 14h00 in the same subplots where biomass was collected. The proportion of light available at ground level was then estimated as the ratio of mean ground level PAR to aboveground PAR.

3.2.4 Statistical analyses

All statistical analyses were conducted in R version 3.5.2. Temporal stability was calculated for each plot over consecutive three year post-treatment periods (i.e. experimental years 1-3; 2-4; 3-5; ...) as the inverse of the coefficient of variation using (3.4)

$$stability = \frac{\bar{x}}{\sigma} \tag{3.4}$$

where $\bar{x}$ is the mean and σ is the standard deviation of ANPP over three years. We used linear mixed-effects models using `lmer` from the `lme4` package for all analyses (Bates et al. 2015). We used the `step` function from the `lmerTest` package for backwards selection of random intercept effects (Kuznetsova et al. 2017). The generic random effect structure initially supplied for all models was treatment year nested within block nested within site; however, this was adjusted to prevent singular fits for some analyses. The resulting random effect structure is described in the model summary table footnotes. We modelled stability by the number of nutrients added (0, 1, 2, 3) as both an ordinal factor and a continuous numeric response. Stability responses were log-transformed to improve residual normality and variance homogeneity. Stability was reduced following nutrient addition (Table 3.A.2) and so for subsequent analyses, we calculated the effect of nutrient addition on the change in stability as the log response ratio (LRR) of the stability response for each nutrient addition treatment to the control stability response within each block. Positive values indicate greater stability following nutrient addition relative to no nutrient addition whilst negative values indicate reduced stability following nutrient addition relative to no nutrient addition.

As grassland communities are often co-limited by multiple nutrients (Harpole et al. 2016), we used treatments where two or three nutrients were added when assessing stability responses to site-level predictors as these nutrient addition levels showed the greatest negative effects on stability. Environmental predictors acting at similar scales were included in the same analysis. We assessed stability responses to geographical position across changes in latitude and elevation. To describe these responses at a finer scale we predicted stability changes across continents. We then modelled changes in stability across three-year means, standard deviations and stabilities of precipitation and potential evapotranspiration (PET). Changes in stability across management regime was the last site-level analysis conducted.

To describe changes in soil properties following nutrient addition we calculated the LRR of the post-treatment soil property value to the pre-treatment soil property value for each plot. All soil property changes were rescaled and included in the same analysis. Only the highest nutrient addition treatment was used in soil property analyses to ensure consistency in the treatment application and to control for possible nutrient co-limitation effects. Only "site" was included as a random intercept for this model as the highest nutrient addition treatment is only applied once per block within each site.

Stability responses to sward characteristics were based on the magnitude of the change in Simpson's diversity (calculated using the `diversity` function from the `vegan` package, Oksanen et al. 2019), species evenness, ground-level light availability and total plant mass of nutrient addition plots compared to no nutrient addition plots as LRRs. We also included the difference in compositional change as the LRR of Bray-Curtis dissimilarities (calculated using the `vegdist` function from the `vegan` package) for nutrient addition plots relative to no nutrient addition plots. Differences in species asynchrony (calculated using the `synchrony` function from the `codyn` package, Hallett et al. 2014) across the first three post-treatment application years as the LRR between nutrient addition plots and no nutrient addition plots was also included in this model. Species richness was not included in this model as its effect on stability is already known to become nullified following eutrophication (Hautier et al. 2014). All nutrient addition levels were included in this analysis to allow for longer sward structure gradients.

Residual normality and variance homogeneity were assessed visually using diagnostic plots. Treatment main effects are presented as mean (95 % Wald confidence intervals). Degrees of freedom are calculated using the Satterwaite method from the `lmerTest` package. Where necessary we tested for the difference in treatment level mean responses to zero using the `emmeans` package (Lenth 2019).

3.3 Results

Over the first three years of the experiment nutrient addition reduced stability (Figure 3.2 and Supplementary Table 3.A.1, $p = 0.043$) with stability reducing as the number of nutrients added increased (Supplementary Table 3.A.2, $p = 0.013$).

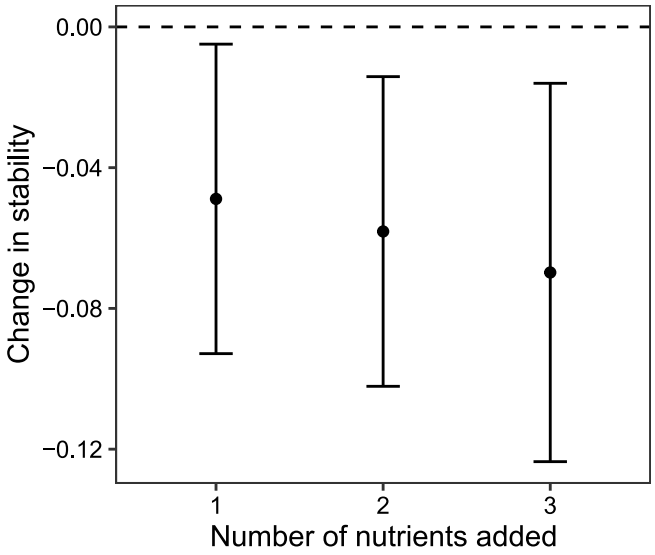

Figure 3.2: The change in temporal stability of grassland total plant biomass across increasing number of added nutrients (number of nutrients = 1,2,3) compared to no nutrient addition. The dotted line represents no change in stability following nutrient addition. Values above and below the dotted line indicate increased and reduced stability following nutrient addition, respectively. Error bars represent 95% confidence intervals.

We studied how these stability changes varied across environmental factors to identify which conditions could predispose grasslands to greater destabilisations. Geographically, stability did not change following nutrient addition across latitude (Figure 3.1, Supplementary Table 3.A.3,

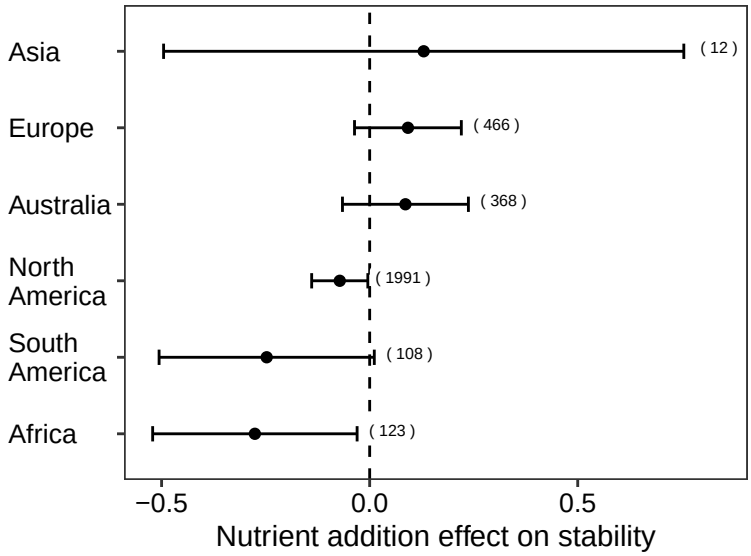

Figure 3.3: Changes in the temporal stability of grassland total plant biomass following belowground nutrient addition (number of nutrients = 2 and 3) compared to no nutrient addition (as the log response ratio) across continents. Numbers in parentheses indicate the number of data points collected for each continent. The dotted line represents no change in stability following nutrient addition. Values to the left and to the right of the dotted line indicate reduced and increased stability in response to nutrient addition, respectively. Error bars represent 95% confidence intervals.

$p = 0.3228$) or elevation (Supplementary Table 3.A.3, $p = 0.7766$). Despite the lack of effects across latitude, there were varying stability responses to nutrient addition across continents ($F_{5,\ 222.0} = 2.814,\ p = 0.017$). African and North American grasslands showed stability reductions following nutrient addition (Figure 3.3) whilst Australian and European grasslands showed more positive responses to nutrient addition than African (the most negatively affected continent) grasslands (Supplementary Table 3.A.4). Across gradients of precipitation and PET temporal means and standard deviations, mean PET explained grassland productivity stability responses to nutrient addition (Supplementary Table 3.A.5). As PET increased grassland stability declined following nutrient addition ($p = 0.020$).

Grassland management was related to stability responses to nutrient addition. Grasslands which have been anthropogenically created were more stable following nutrient addition than when no nutrients were added (Figure 3.4 and Supplementary Table 3.A.6, $p = 0.005$). However, in combination with burning, belowground nutrient addition reduced stability compared to no nutrient addition (Figure 3.4 and Supplementary Table 3.A.6, $p = 0.004$). Whether a grassland was grazed by herbivores ($p = 0.942$) or mowed ($p = 0.947$) did not influence grassland stability responses to nutrient addition (Figure 3.4 and Supplementary Table 3.A.6).

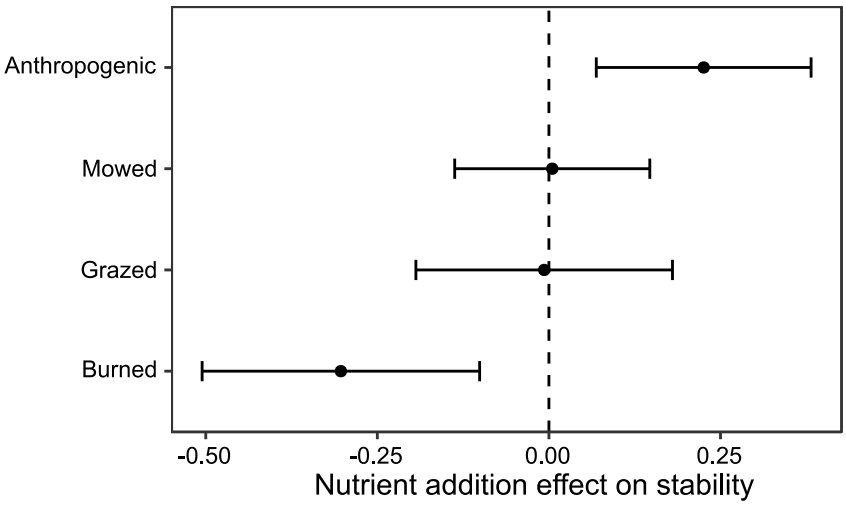

Figure 3.4: Changes in the temporal stability of total plant biomass across grassland management regimes as the log response ratio of belowground nutrient addition (number of nutrients = 2, 3) compared to no nutrient addition. The dotted line represents no change in stability following nutrient addition. Values to the left and to the right of the dotted line indicate reduced and increased stability in response to nutrient addition, respectively. Error bars represent 95% confidence intervals.

We also found that changes in stability following nutrient addition covary with changes in some soil properties (Figure 3.5, Supplementary Table 3.A.7). Stability was promoted following increases in soil pH ($p = 0.015$) and CEC ($p = 0.028$). Reduced stability of nutrient enriched grasslands compared to control grasslands was associated with increased soil potassium ($p = 0.041$) and calcium ($p = 0.024$). All other soil properties varied inconsistently stability changes following nutrient addition.

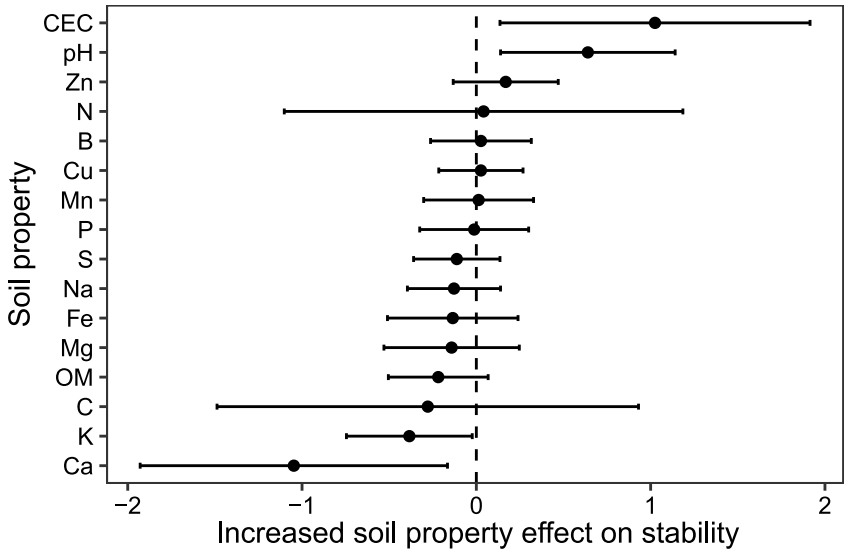

Figure 3.5: Scaled changes in the temporal stability of total plant biomass as a function of changes in soil properties as the log response ratio of belowground nutrient addition (number of nutrients = 3) compared to no nutrient addition. The dotted line represents no change in stability following nutrient addition. Values to the left and to the right of the dotted line indicate reduced and increased stability, respectively, when nutrient additions increase the value of the soil property. Error bars represent 95% confidence intervals. CEC - cation exchange capacity, OM - organic matter.

Sward structure changes between year 0 and year 3 (Bray-Curtis dissimilarity, community evenness, Simpson's diversity, total plant mass, ground level light availability) and across the first three post treatment years (species asynchrony) relative to control plots were also considered as potential predictors of change in stability following nutrient addition. When nutrient addition reduced species asynchrony compared to control grassland species asynchrony, nutrient enrichment reduced grassland stability (Figure 3.6 and Supplementary Table 3.A.8, $p < 0.0001$). Increased compositional dissimilarity induced by nutrient enrichment reduced grassland stability compared to control grasslands (Figure 3.6 and Supplementary Table 3.A.8, $p = 0.0004$). Increased plant community evenness between year 0 and year 3 of nutrient enriched plots relative to control plots also reduced nutrient enriched grassland stability relative to control plots (Figure 3.6 and Supplementary Table 3.A.8, $p = 0.032$). Neither Simpson's diversity ($p = 0.411$), total plant mass ($p = 0.771$), nor ground level light availability ($p = 0.270$) changes were associated with stability responses to nutrient addition (Figure 3.6 and Supplementary Table 3.A.8).

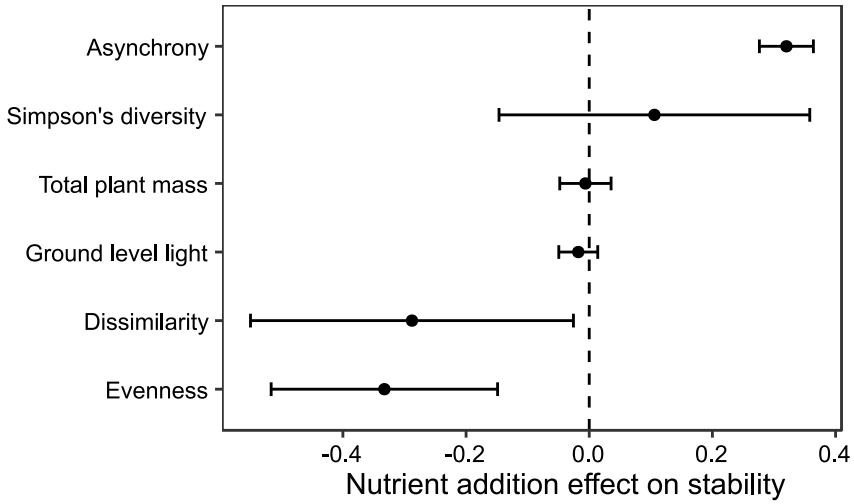

Figure 3.6: Changes in temporal stability of total plant biomass across changes in grass sward characteristics as the log response ratio of nutrient addition (number of nutrients = 1, 2, 3) compared to no nutrient addition. The dotted line represents no change in stability following nutrient addition. Values to the left and to the right of the dotted line indicate reduced and increased stability in response to nutrient addition, respectively. Error bars represent 95% confidence intervals.

3.4 Discussion

We found that reducing belowground nutrient competition through nutrient addition had an increasingly negative effect on biomass stability. However, this effect was not consistent across environmental factors. Some environmental factors (e.g. elevation, precipitation, defoliation, physical sward characteristics changes) inconsistently influenced stability following nutrient addition whilst other environmental factors either reduced (e.g. burning regime, increased soil K and Ca, species compositional change, increased evenness) or promoted (e.g. latitude, longitude, anthropogenic influence in grassland history, increased soil CEC and pH, increased species asynchrony) stability following nutrient addition.

3.4.1 Topography and climate

Globally, more positive stability responses to nutrient addition occurred at higher latitude grasslands. This is likely due to increased nitrogen limitation occurring at higher latitudes possibly driven by temperature-induced belowground nutrient limitation (Fay et al. 2015). At lower latitudes, nutrient addition has a less positive effect on productivity but as latitude increases so too does fertiliser's effect on biomass production (Fay et al. 2015). This increase in mean biomass production could result in increased grassland stability in high latitude grasslands. However, given that there is no change in stability despite potential changes in mean production, it is likely that the variation around mean production scales proportionately as latitude increases. The responses observed for Asian grasslands are likely not representative of the continent. Despite a poor representation in this experiment other recent work has shown that western Asian grassland biomass is also controlled by nutrient limitation (Palpurina et al. 2019) and that grassland stability tends to decline following nutrient addition (Yang et al. 2012).

As PET increases plants become more stressed due to a greater water availability deficit

(Droogers and Allen 2002; Zwicke et al. 2013). Grassland productivity is known to increase along experimentally created grassland diversity gradients under either nutrient addition or water limitation (Craven et al. 2016) although these relationships may not always be detected in natural settings (Dormann et al. 2017). If diversity does positively affect productivity during climatic stress, diversity could have a stabilising effect on biomass production (Haughey et al. 2018). As climatic stress reduced grassland productivity the stabilising effects of diversity will likely be lower for stressed communities compared to control communities (Craven et al. 2016; Haughey et al. 2018). Our results (together with those from Nogueira et al. 2018) show that nutrient deposition combined with climatic stress have additive (albeit weak) negative effects on grassland community stability.

3.4.2 Management regime

Grassland management can also influence grassland stability responses to nutrient addition. Nutrient enriched anthropogenically created grasslands experienced increased stability following nutrient addition. This is a promising finding given the negative impacts of increased land-use intensity on biodiversity-ecosystem functioning and stability (Blüthgen et al. 2016). However, anthropogenically influenced grasslands are generally less diverse which is an important constraint to successful restoration (Walker et al. 2004). Nutrient addition as a solution for stabilising anthropogenic grasslands is unlikely to be a sustainable long-term solution as impacts from nutrient addition reduce diversity as well as the likelihood of colonisation events (Blomqvist et al. 2003; Hautier et al. 2009; Isbell et al. 2013b). However, if the goal of restoration is ecosystem function stability of one or a few selected functions instead of increased diversity and multifunctionality, maintaining these artificial grasslands through nutrient addition could contribute towards meeting this specific outcome.

Reduced stability of nutrient enriched, burnt grasslands could result from an increased disturbance magnitude. Although disturbance can promote species diversity and community functioning (van der Maarel 1993) and fire often maintains the grassland ecosystem state (Van Langevelde et al. 2003; Bond et al. 2004), multiple disturbance types can produce interacting effects (Koerner et al. 2014; Koerner and Collins 2014; Wright et al. 2015). Furthermore, greater fire and nutrient addition frequencies can change community structure and diversity independently (Leonard et al. 2010; Hovick et al. 2015; Ward et al. 2017) which (particularly in the case of nutrient addition) predisposes plant communities to instability (MacDougall et al. 2013; Hautier et al. 2015). Our results show that a strong interaction exists between fire and eutrophication in grasslands and we caution against increasing the nutrient availability of grasslands which have a burning regime.

Defoliation by grazing or mowing did not influence stability changes in response to nutrient addition. This was surprising given that fire and herbivory are believed to exhibit similar characteristics and effects (Bond and Keeley 2005). However, differences exist in the time that grazing/mowing and fire occur which could have influenced these stability outcomes. Grazing and mowing generally take place throughout the growing season whilst fire is generally applied in late winter or the early growing season which allows for plant biomass to accumulate during the growing season and potentially shade out subordinate species. Furthermore, mowing and herbivory can increase grassland structural spatial homogeneity but can also reduce species dominance (Lepš 2014; Mortensen et al. 2018). As defoliation also increases light availability (Borer et al. 2014b), it is likely that, despite these higher nutrient availabilities, smaller species were able to persist (Hautier et al. 2009). This likely prevented species compositional change following nutrient addition and with that changes in stability. The absence of an effect could

also have arisen from the methodology used in this experiment. Removing biomass during the growing season could have influenced our results. As the stability metric used in these analyses is based on aboveground plant biomass collected at the end of the growing season, treatments which directly manipulate this biomass during the period when it is produced could confound the metric. Other metrics of stability such as species asynchrony or cumulative biomass sampling could potentially overcome this issue.

3.4.3 Soil property changes

Fertiliser addition also affected ecosystem stability through changes in soil nutrient availability. Interestingly, grasslands with high soil pH can have lower productivity (Stevens et al. 2015) with some nutrient enriched grasslands showing a negative relationship between nutrient addition intensity and soil pH (Zhang et al. 2015). Despite potentially lower productivity at higher pH, productivity may have been stabilised because nutrients become more equally available to other community members thereby allowing them to coexist with other more competitive species.

Nitrogen and phosphorus have often been shown to play important roles in grassland nutrient limitation (Elser et al. 2007; Li et al. 2016). However, in our study Ca (likely resulting from P addition) and K increases were associated with reduced stability in fertilised grasslands highlighting the role of macronutrient but not necessarily micronutrient limitation for stabilising grassland productivity. Potassium and micronutrients are relatively understudied as a soil nutrient but exploratory studies have suggested that these elements can play an important role in the nutrient limitation of grassland productivity (Fay et al. 2015; Harpole et al. 2016). Over time, however, our results show that the effects of commonly studied nutrients (e.g. C and N) have varying effects when productivity variation is incorporated. A closer investigation of the temporal productivity responses to environmental conditions from a nutrient limitation perspective could provide further insight.

3.4.4 Sward structure and diversity changes

Changes in physical sward characteristics (total plant mass, ground-level light availability) over the first three years of nutrient addition appear to be unimportant to ecosystem stability following nutrient addition. Biomass changes could affect stability in different ways. The first is through lower light availability which reduces species richness (Borer et al. 2014a) and the likelihood of species colonisation events (Hautier et al. 2009) thereby resulting in biodiversity reductions. However, Hautier et al. (2014) showed that positive effects of species richness on stability are nullified following nutrient addition. The other way physical characteristics could affect stability is through increased mean biomass production which, if coupled with proportionately smaller increases in biomass production variability, would increase stability. Given that diversity changes become magnified through time (Harpole et al. 2016), direct effects of biomass and light on stability (through changes in diversity) may only be detected during later years of this experiment.

Because changes in physical sward characteristics (species richness changes) do not explain community stability responses and because species richness measurements potentially hide underlying fluctuations in grassland communities (Jones et al. 2017), incorporating species identity into diversity metrics yielded important insight. Our compositional similarity results are in line with Allan et al. (2015) and Melts et al. (2018) who found that minimising species compositional change through time maintains ecosystem stability and functioning. This suggests that changes in community composition could lead to periods of instability.

Contributions to grassland functioning by dominant plant species have also long been realised (McNaughton and Wolf 1970), and recent evidence has highlighted the importance of these dominant species in response to environmental change (Loreau et al. 2001; Smith and Knapp 2003; Allan et al. 2011; Fynn et al. 2011; Koerner and Collins 2014; Xu et al. 2015; Avolio et al. 2019). Our results which indicated that increased species evenness also destabilised plant communities provide global corroboration of these studies. Taking our evenness and compositional change effects on grassland responses to nutrient addition together suggests that dominant species persistence may be what improves community stability through anthropogenic change. This appears to challenge Allan et al. (2011) who alternatively proposed that dominant species turnover during environmental changes is what promotes community stability. Contrasting our and their experimental designs revealed that over longer periods (e.g. measuring compositional change over seven years as Allan et al. (2011) did) changes in dominant species identity may become more important.

Hautier et al. (2014) showed that nutrient addition does not affect the relationship between stability and asynchrony. Our results expand on this by showing that should increased species asynchrony coincide with nutrient addition, community stability will also increase. This also complements recent work which highlighted that maintaining spatial species asynchrony also maintains stability in nutrient enriched grasslands (Zhang et al. 2019). Again, taken together with our observed changes in compositional dissimilarity and evenness, these results paint an almost contradictory picture - if communities are to resist impacts of anthropogenic change they will need to need to become less even and more asynchronous. The ideal scenario could therefore be highly uneven communities composed of many rare species. Yang et al. (2017) explored dominant and rare species contributions to community stability and showed that reductions in subordinate (but not rare) species stability can reduce community stability. Functions provided by rare species can be very important to the community (Soliveres et al. 2016b; Yang et al. 2018) but whether rare species are important globally and how (if at all) rare species contribute towards community stability across environmental factors remains unknown.

3.4.5 Conclusion

This study has highlighted several important drivers of grassland production stability in response to increased levels of nutrient addition across the globe. Grassland stability responses to nutrient addition are dependent on and are driven by many factors. Some of these factors are fixed (such as location) and so human impacts in African and North American grasslands should be minimised. Our results also stress the importance of minimising human impacts on natural grasslands more so than on anthropogenically created grasslands, particularly those natural grasslands where burning regimes are part of the management regime. Furthermore, this work has provided general support for the importance of uneven communities for resisting global change drivers. A hypothesis relating to how dominant and rare species responses to global change could affect plant community stability outcomes is also proposed.

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Supplementary materials

3.A Supplementary tables

Supplementary Table 3.A.1: Statistical model for the effect of the number of nutrients added (nnut, as a categorical predictor) on the temporal stability total plant mass stability. Positive responses indicate improved stability following nutrient addition as the predictor increases. Negative responses indicate reduced stability following nutrient addition as the predictor increases. Temporal stability was measured over consecutive three year periods as the ratio of the mean total plant mass to the variation of total plant mass

	Value	SE	DF	t-value	p-value
(Intercept)	1.106	0.045	84.3	24.751	<0.0001
nnut1	-0.049	0.022	5038.0	-2.178	0.0294
nnut2	-0.058	0.022	5039.0	-2.589	0.0096
nnut3	-0.070	0.027	5033.8	-2.544	0.011

Linear mixed-effects model of log transformed stability responses was fit by restricted maximum likelihood. t-tests were conducted using the Satterwaite method. Random intercepts effects included in the model were 'site' (s.d. = 0.296), and 'year within block within site' (s.d. = 0.292). The intercept is the estimated mean value of the control plots (no nutrients added). This model is shown in Figure 3.2.

Supplementary Table 3.A.2: Statistical model for the effect of the number of nutrients added (nnut, as a continuous predictor) on the temporal stability total plant mass stability. Positive responses indicate improved stability following nutrient addition as the predictor increases. Negative responses indicate reduced stability following nutrient addition as the predictor increases. Temporal stability was measured over consecutive three year periods as the ratio of the mean total plant mass to the variation of total plant mass

	Value	SE	DF	t-value	p-value
(Intercept)	1.087	0.043	69.1	25.564	<0.0001
nnut	-0.020	0.008	5038.7	-2.492	0.0127

Linear mixed-effects model of log transformed stability responses was fit by restricted maximum likelihood. t-tests were conducted using the Satterwaite method. Random intercepts effects included in the model were 'site' (s.d. = 0.296), and 'year within block within site' (s.d. = 0.292). The intercept is the estimated mean value of the control plots (no nutrients added).

Supplementary Table 3.A.3: Statistical model for the effects of elevation above sea level (in meters) and geographical coordinates on the effect of belowground nutrient addition (number of nutrients = 2, 3) on the of total plant mass temporal stability relative to no nutrient addition as log response ratios. Positive responses indicate improved stability following nutrient addition as the predictor increases. Negative responses indicate reduced stability following nutrient addition as the predictor increases. Temporal stability was measured over consecutive three year periods as the ratio of the mean total plant mass to the variation of total plant mass

	Value	SE	DF	t-value	p-value
(Intercept)	-0.056	0.043	178.0	-1.303	0.1943
elevation	0.000	0.000	193.1	-0.284	0.7766
latitude	0.001	0.001	176.1	0.992	0.3228

Linear mixed-effects mode was fit by restricted maximum likelihood. t-tests were conducted using the Satterwaite method. Random intercepts effects included in the model were 'block within site' (s.d. = 0.252), and 'year within block within site' (s.d. = 0.410). The intercept is the estimated mean stability response to nutrient addition where all predictors are equal to zero.

Supplementary Table 3.A.4: Statistical model for the effects of the effect of belowground nutrient addition (number of nutrients = 2, 3) on the of total plant mass temporal stability relative to no nutrient addition as log response ratios across continents. Positive responses indicate improved stability following nutrient addition on the continent. Negative responses indicate reduced stability following nutrient addition on the continent. Temporal stability was measured over consecutive three year periods as the ratio of the mean total plant mass to the variation of total plant mass

	Value	SE	DF	t-value	p-value
(Intercept)	-0.276	0.125	246.9	-2.214	0.028
continentAsia	0.406	0.342	556.9	1.187	0.236
continentAustralia	0.362	0.146	216.4	2.475	0.014
continentEurope	0.368	0.141	239.9	2.617	0.009
continentNorth America	0.204	0.129	236.4	1.580	0.116
continentSouth America	0.028	0.181	216.7	0.157	0.875

Linear mixed-effects mode was fit by restricted maximum likelihood. t-tests were conducted using the Satterwaite method. Random intercepts effects included in the model were 'site' (s.d. = 0.253), and 'year within block within site' (s.d. = 0.411). The intercept is the estimated mean stability response to nutrient addition for African sites. This model is shown in Figure 3.3.

Supplementary Table 3.A.5: Statistical model for the effects of climatic stability on stability responses to belowground nutrient addition (number of nutrients = 3) on the total plant mass temporal stability relative to no nutrient addition as log response ratios. Positive responses indicate improved stability following nutrient addition as the predictor increases. Negative responses indicate reduced stability following nutrient addition as the predictor increases. Temporal stability was measured over consecutive three year periods as the ratio of the mean total plant mass to the variation of total plant mass

	Value	SE	DF	t-value	p-value
(Intercept)	0.370	0.204	70.4	1.810	0.075
ppt.mean	0.000	0.000	60.1	-1.094	0.278
ppt.sd	0.000	0.000	415.5	-0.267	0.79
pet.mean	0.000	0.000	55.8	-2.392	0.02
pet.sd	0.000	0.000	390.3	1.077	0.282
ppt.stab	-0.005	0.006	495.0	-0.841	0.401
pet.stab	0.001	0.001	520.8	0.546	0.585

Linear mixed-effects mode was fit by restricted maximum likelihood. t-tests were conducted using the Satterwaite method. Random intercepts effects included in the model were 'site' (s.d. = 0.217), and 'year within site' (s.d. = 0.629). The intercept is the estimated mean stability response to nutrient addition where all predictors are equal to zero. ppt - Precipitation; pet - Potential evapotranspiration.

Supplementary Table 3.A.6: Statistical model for the effects of higher levels of belowground nutrient addition (number of nutrients = 2, 3) on the change total plant mass temporal stability relative to no nutrient addition as log response ratios across grassland management regimes. Positive responses indicate increased stability following nutrient addition under a management regime. Negative responses indicate reduced stability following nutrient addition under a management regime. Temporal stability was measured over only the first consecutive three year period following treatment application as the ratio of the mean total plant mass to the variation of total plant mass

	Value	SE	DF	t-value	p-value
(Intercept)	-0.057	0.033	139.8	-1.735	0.085
anthropogenicYes	0.226	0.080	274.9	2.824	0.005
burnedYes	-0.303	0.103	249.8	-2.939	0.004
grazedYes	-0.007	0.095	282.6	-0.072	0.942
managedYes	0.005	0.073	210.7	0.067	0.947

Linear mixed-effects mode was fit by restricted maximum likelihood. t-tests were conducted using the Satterwaite method. Random intercepts effects included in the model were 'block within site' (s.d. = 0.253), and 'year within block within site' (s.d. = 0.410). The intercept is the estimated mean stability response to nutrient addition where no management regime was present. This model is shown in Figure 3.4.

Supplementary Table 3.A.7: Statistical model for the effects of only the highest level of belowground nutrient addition (number of nutrients = 3) on the change total plant mass temporal stability relative to no nutrient addition as log response ratios across changes in soil properties. Changes in soil properties were calculated as the scaled log response ratio of the property between the pre- and post-treatment responses. Positive responses indicate increased stability following nutrient addition as the value of the soil property increased with time. Negative responses indicate reduced stability following nutrient addition as the value of the soil property increased with time. Temporal stability was measured over only the first consecutive three year period following treatment application as the ratio of the mean total plant mass to the variation of total plant mass

	Value	SE	DF	t-value	p-value
(Intercept)	-0.006	0.136	13.9	-0.041	0.968
CEC	1.025	0.454	50.6	2.259	0.028
OM	-0.218	0.146	22.5	-1.496	0.149
pH	0.640	0.256	62.7	2.504	0.015
C	-0.279	0.617	68.3	-0.452	0.653
N	0.041	0.583	51.2	0.071	0.944
P	-0.012	0.159	54.8	-0.078	0.938
K	-0.384	0.184	63.7	-2.088	0.041
B	0.026	0.147	37.0	0.179	0.859
Ca	-1.047	0.450	55.6	-2.328	0.024
Cu	0.026	0.123	37.7	0.212	0.833
Fe	-0.135	0.191	34.0	-0.708	0.484
Mg	-0.142	0.198	49.3	-0.716	0.478
Mn	0.013	0.161	55.3	0.081	0.936
Na	-0.128	0.136	49.0	-0.942	0.351
S	-0.112	0.126	23.0	-0.887	0.384
Zn	0.169	0.154	38.7	1.097	0.28

Linear mixed-effects mode was fit by restricted maximum likelihood. t-tests were conducted using the Satterwaite method. 'Site' (s.d. = 0.374) was included as a random intercept for this model. The intercept is the estimated mean stability response to nutrient addition where no change across all soil properties was detected. This model is shown in Figure 3.4.

Supplementary Table 3.A.8: Statistical model for the effects of all levels of belowground nutrient addition (number of nutrients = 1, 2, 3) on the change total plant mass temporal stability relative to no nutrient addition as log response ratios across changes in grass sward properties. Changes in grass sward properties were calculated as the log response ratio of the property between the pre- and post-treatment responses. Positive responses indicate increased stability following nutrient addition as the value of the sward property increased with time. Negative responses indicate reduced stability following nutrient addition as the value of the sward property increased with time. Temporal stability was measured over only the first consecutive three year period following treatment application as the ratio of the mean total plant mass to the variation of total plant mass

	Value	SE	DF	t-value	p-value
(Intercept)	-0.127	0.045	332.6	-2.791	0.006
bray.curtis	-0.134	0.040	2098.6	-3.371	0.001
evenness	-0.293	0.134	2078.0	-2.188	0.029
simpson	0.124	0.128	1715.8	0.966	0.334
total.mass	-0.007	0.021	1306.7	-0.328	0.743
pro.par	-0.016	0.016	1272.2	-1.013	0.311
async	0.322	0.022	2339.2	14.349	<0.0001

Linear mixed-effects mode was fit by restricted maximum likelihood. t-tests were conducted using the Satterwaite method. 'Block within site' (s.d. = 0.279) was included as a random intercept for this model. The intercept is the estimated mean stability response to nutrient addition where no change across all sward properties was detected. This model is shown in Figure 3.6.

Chapter 4

Conclusion

> *For in him all the fullness of God was pleased to dwell, and through him to reconcile to himself all things, whether on earth or in heaven, making peace by the blood of his cross.*
>
> – Paul the apostle, Colossians 1:19-20

4.1 Introduction

The manuscripts contained in this dissertation have explored many facets of grassland ecosystem stability. The high-level overview generated through a quantitative synthesis of review publications addressing aspects relating to grassland ecosystem stability (Chapter 1) showed clearly how complex (and often unclear) ecological interactions are within the grassland ecosystem. Furthermore, it emphasised the breadth and depth of knowledge available on the functioning of the grassland ecosystem. However, it also brought to light some important areas where this knowledge has not been effectively communicated to those involved in policy decision making. As the ecological processes which contribute to sustaining global processes are faced with increasing strain, academics and policy makers will need to collaborate more effectively, especially on issues where there is strong academic consensus paired with globally replicated observational and experimental evidence.

Despite there being several areas which are well represented within the grassland stability literature, there were several important knowledge gaps identified through the examination of published reviews. This informed the local assessment of grassland ecosystem stability responses to the combined effects of nutrient enrichment and temperature stress (Chapter 2). The somewhat unexpected findings from this research raised new questions relating to the resilience of less diverse anthropogenically modified grasslands which, despite being highly productive under some disturbances (such as high temperature stress), may not be able to persist as well as more diverse grassland communities under other combinations of disturbances such as fire in combination with high temperature stress. A strong theme of this work was that at both the grassland productivity and climate levels it was the variability (rather than the magnitude) of ecosystem processes that were important. By unpacking the variability associated with ecosystem processes, future studies may reveal new insights to further explain ecosystem dynamics in response to global change.

The second experimental investigation of this dissertation explored grassland ecosystem stability responses to nutrient enrichment across various environmental gradients (Chapter 3). Encouragingly, several aspects of this study aligned with the common themes identified during

the examination of published review articles (Chapter 1). Whilst nutrient enrichment had a general destabilising effect on grasslands, there were some circumstances where grasslands tended to respond positively to nutrient addition. Under careful consideration, grasslands with these conditions could potentially benefit from nutrient enrichment in the form of herbivore mediated redistributions, eutrophication via atmospheric deposition or run-off, provided there are processes implemented to maintain nutrient cycling and minimise nutrient losses to other nutrient sensitive ecosystems. However, we stress that those grassland systems which have been largely protected from anthropogenic activity should remain so to avoid restorative action in the future. Apart from the currently acknowledged drivers of grassland stability identified in Chapter 1, this work highlighted the sensitivity of fire-controlled systems to anthropogenic activity, whilst emphasising that the finer aspects of diversity (asynchrony and compositional and dominance shifts) help to further explain grassland stability responses to fertilisation. Whilst there were hints of these aspects of grassland ecosystems influencing stability identified in Chapter 1, they tended to be in the minority (except for perhaps compositional shifts in the form of either plant invasions or woody encroachment).

4.2 Aims and objectives

The aim of this dissertation was to firstly assess, then to expand, and finally to corroborate our understanding of grassland ecosystem stability in light of recent theses which have attempted to refine our understanding of grassland ecosystem functioning. This was successfully achieved through systematically mapping out the current state of the art of the grassland biodiversity-stability-ecosystem functioning literature. Based on the findings of this exercise, the subsequent aspects of this dissertation contributed to our understanding of grassland ecosystem stability responses to the combined effects of climate variability and nutrient enrichment - an important knowledge gap identified during the review mapping process. The final aspect of this dissertation then provided experimental and corroborative evidence of the responses of grassland stability to anthropogenic activity.

4.3 Challenges

One of the biggest challenges realised through this dissertation is that mapping out a whole discipline of grassland research be a long-term project unless many people become involved in the project. However, the attempt at mapping review publications provided some insight into the common themes discussed in the discipline which could inform future, more focussed mapping studies. Another challenge that was identified was calculating stability in situations where the ecosystem function or process is directly affected by a treatment. In these cases the stability calculation is unlikely to provide useful information and so alternative metrics should be considered.

4.4 Future possibilities

The under-representation of land-use impacts on grassland stability within review publications should be of great concern. This is especially true because of the dramatic and direct effects that land-use change has on grassland biodiversity, stability and ecosystem functioning. Future explorations into the mechanisms underpinning grassland responses to land-use change (especially on global scales - e.g. the recently initiated dragnet (`http://www.nutnet.org/dragnet`) experiment) will greatly inform future biodiversity

conservation efforts and policy decisions in both direct and practical manners.

For exploratory purposes, the analyses of the globally replicated nutrient addition experiment (Chapter 3) only considered the main effects of environmental gradients. This revealed which conditions likely control grassland ecosystem stability responses to human impacts. However, these conditions are unlikely to exist in isolation. Based on the findings of this work, future studies could explore how grassland stability responds to nutrient enrichment across interacting environmental gradients in a similar vein to the analyses presented in Chapter 2.

4.5 Final comments

The initial ideas proposed in the introduction of Chapter 1 were a somewhat bold attempt at expanding the horizons of a fundamental aspect of grassland ecology. This work has shown that, although challenging, the state of the art of a discipline can be assessed in a systematic way to identify areas of consensus, confusion, uncertainty. Furthermore, it has drawn our attention to some surprising results relating to anthropogenically modified grasslands which perhaps provide more questions than answers. Finally, through a globally replicated experiment, it was shown that there are scientific paradigms which are both corroborated and not corroborated by experimental observations. There are also several aspects, particularly soil-plant interactions, which are markedly underrepresented in the grassland biodiversity-stability-ecosystem functioning domain.